COMMUNITY INTERACTIONS AND IMPACTS OF EXOTIC PLANT SPECIES IN THE SOUTHEASTERN UNITED STATES

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A dissertation submitted to the faculty at the University of North Carolina at Chapel Hill in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Curriculum for the Environment and Ecology.

Chapel Hill
2016

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ABSTRACT

Dennis Darwin Tarasi: Community interactions and impacts of exotic plant species in the southeastern United States.
(Under the direction of Robert K. Peet)

Native to other regions of the world, exotic species can disrupt the ecology and function of natural areas where they are introduced. Exotic species successfully establish in and dominate natural areas via multiple pathways and ecological processes. Given that many of these interactions remain difficult to measure, it is imperative to properly identify environmental factors that predict exotic species success and quantify the impacts of exotic species dominance on natural communities. Here, I explore the interactions between exotic plant species and communities where they have been introduced in the southeastern United States to address the predictors of invasion, community responses to invasion and subsequent removal of dominant invaders. Chapter 2 considers whether biotic communities predictably incorporate or resist exotic species by examining the relationship between native species richness and exotic species richness at multiple spatial scales across a broad range of environmental conditions. Chapter 3 explores the predictive ability of environmental characteristics concerning exotic species success in a large vegetation database. Chapter 4 quantifies the abiotic and biotic community changes with invasion of a dominant exotic shrub, including assessments of species diversity and the physical structure of the community. Chapter 5 assesses the abiotic community differences resulting from exotic

shrub invasion, including abiotic responses to removal of that dominant shrub from the community.

Exotic species success generally and predictably responds to changes in the scale of observation and local environmental conditions. Several environmental characteristics correlate with exotic species success, including soil pH, calcium, tree stem density and cover of wetland species. The unique predictive ability of any individual variable remains limited, reflecting the complex interactions driving exotic species success and the differences among exotic species. Invaded communities exhibit several distinct responses to exotic species dominance, including changes in both richness and physical forest structure. Such changes must be considered in context, as invaders of similar structure, function and origin differentially affect the communities they invade. Although shrub invasions, and the subsequent removal of dominant invaders, may cause demonstrable abiotic changes in the community, such as in temperature and light availability, responses in soil moisture and nutrient levels are limited.

ACKNOWLEDGEMENTS

I am fortunate beyond measure to have chosen an excellent mentor in my dissertation advisor, Robert K. Peet. You have demonstrated to me the enduring commitment, dedication and service that make you a role model for many scientists. You have provided me with the structure to understand the rigors of scientific research, the patience and willingness to hear out my research ideas, and the trust to let me succeed (and fail!) on my own in data collection and analysis. I hope to emulate your service and mentorship in my own academic career.

I owe a significant amount of gratitude to my academic committee: John Bruno, Alan Weakley, Peter White, and Justin Wright. Your continued support aided tremendously in my professional development and exploration of research questions, and much of this dissertation stems directly from suggestions you made during committee meetings and personal conversations. I was additionally fortunate to have found multiple role models of academic success while at UNC, particularly Corey Johnson, Steve Matson, Charles Mitchell and Patricia Gensel, among many others. Your example and interactions with me have provided a clear model for my career goals. Thank you all for you time and effort in supporting me.

I relied on many peers in developing my research ideas and manuscripts, and I thank them for their tireless support in providing edits and suggestions for my research. I was fortunate to gain insights from and share successes with Bianca Lopez, Peter Wilfahrt and Sierra Woodruff in our dissertation writing group. Many members of the UNC Plant Ecology

Lab, particularly Alissa Brown and Michael Lee, have graciously provided countless helpful comments of each of my chapters.

I have been fortunate, in my time at UNC, to be a part of a very special, interdisciplinary program. The UNC Curriculum for the Environment and Ecology has exposed me to many more different styles of thought, content subjects, and scientific thinkers than I expected upon entering graduate school. I am truly humbled to be a small part of such a fantastic program, and I thank Jaye Cable, Mike Piehler, Kathleen McNeil and Violet Anderson for their efforts in coordinating and improving the program throughout my time here. I additionally received considerable support, in funding, training and institutional resources from the UNC Department of Biology, the UNC Graduate School and the UNC Graduate and Professional Student Federation.

My dissertation fieldwork would not have been possible without the assistance of numerous volunteer field researchers. I sincerely thank Victoria Millsap, Daniel Tarasi, Shakira Marshall and Braedon Shelton for assistance with data collection during summer 2014, and Jessica Richmond, Chris Boling, and Taek Lee for assistance with my exotic removal experiment during summer 2015. I hope our work together helps lead you to much success in your career pursuits, much as you all have helped me.

In addition to my field assistants, I was fortunate to make connections through my advisor with several fantastic conservation leaders. Andy Kane, Haywood Rankin and Amy Nason assisted me tremendously in identifying and selecting communities for my field studies, as well as sharing their wisdom and resources in response to any request I made. Their knowledge and support in gaining access to these lands was critical to my successful field seasons, and I cannot thank them enough for all their help. I also recognize and

appreciate the Allen Hurlbert lab for graciously loaning me their HOBO trackers for use during the 2015 field season.

I thank Robert Peet, Thomas Wentworth, Michael Schafale and Alan Weakley, who coordinated the Carolina Vegetation Survey (CVS), as well as the countless volunteers who assisted with data collection and entry. Michael Lee was integral in helping me extract data from the CVS database for my analyses. Without their efforts, much of my dissertation research would not have even been possible. I truly stand on the shoulders of giants. I additionally relied on Jack Weiss and James Umbanhowar for suggestions and support regarding several statistical analyses.

My siblings Frank, Julie and Daniel Tarasi, with members of my extended family, have helped ground me in what is truly important in life. Thank you each for exploring the world with me growing up, challenging my perspective and worldview, and making the effort to be a part of my life and graduate career, even at a great distance from home. I love you and yours, very much.

My wife, Megan Tarasi, has provided constant and positive support in all my graduate pursuits. From assisting me late in the night with soil sample analysis, to attending and participating in the academic activities I helped organize, to hearing out and editing countless manuscripts, proposals, and ideas, you have helped me grow in my scientific efforts through your unbounding support for everything that I undertook. I am so incredibly excited by the direction our journey together takes us beyond Chapel Hill.

Finally, I dedicate this dissertation to my parents, Susan M. Tarasi and the late Frank L. Tarasi III. From you I gained the sense of curiosity and exploration that led me to biology, ecology and my graduate pursuits. Words will never suffice to express my gratitude for your

untold sacrifice for me to pursue my dreams, as well as your unconditional love and support in all pursuits that I've undertaken and mistakes I've made along the way. I hope to live my life and love my family in your example, and I sincerely could never thank you enough. I love you both, so much.

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CHAPTER 1: INTRODUCTION

In his seminal work *On the Origin of Species,* Charles Darwin (1859) articulated to the scientific community the concept of interactions between species from different regions of the world. According to Darwin's "naturalisation hypothesis," species introduced to new ecological communities would be most successful in surviving if they were biologically unrelated to the resident species, thus exploiting different resources and life history traits (Rejmánek 1996). Although the concepts of vacant niches and species invasions had gained significant traction in ecological study (e.g. Hutchinson 1957), the study of invasive exotic species as an ecological sub-discipline truly began with Charles Elton's (1958) exploration of the differential ecological interactions between species with shared and varying evolutionary histories.

Since Elton's publication, invasive exotic species have gained substantial attention from academics and conservationists alike, corresponding to their listing as one of the greatest threats to global biodiversity (Wilcove et al. 1998) and reflected in an exponential increase in publications on the topic (Richardson and Pyšek 2008). Researchers have defined the unique stages of successful invasions (e.g. Theoharides and Dukes 2007, Rejmánek et al. 2013) and explored nearly every aspect of these stages, both from the perspective of successful invaders and of communities experiencing invasion. For example, academic publications on exotic species have employed experimental, observational and theoretical methods to address such topics as:

-Introduction pathways of exotic species (e.g. Reichard and White 2001, Lehan et al. 2013),

-Species traits that enable successful establishment in novel environments (e.g. Richardson et al. 2000, Tilman 2004, Pyšek and Chytrý 2014),

-Environmental and community conditions that are most susceptible to species invasions (e.g. Fridley et al. 2004, Herben et al. 2004, Stohlgren et al. 2008, Catford et al. 2012),

-Environmental and ecological impacts of species invasions (e.g. Vila et al. 2011, Powell et al. 2013, Simberloff et al. 2013, Stohlgren and Rejmánek 2014), and

-Community responses to removal of invasive species (e.g. Flory and Clay 2009, Buckley and Han 2014).

Although the body of literature concerning exotic species is both robust and growing, general conclusions associated with species invasions remain elusive (e.g. Catford et al. 2011) or controversial (e.g. Gurevitch and Padilla 2004, Clavero and Garcia-Berthou 2005). Because of these inconsistencies and challenges, continued research on species invasions remains paramount to the pursuit of greater ecological understanding.

For my dissertation research, I explored several questions foundational to the understanding of native community impacts from and interactions with introduced exotic species. Countless dissertations could be developed on invasive species and community ecology topics not considered in this document, such as enemy release, rapid evolution, transformation of ecosystem conditions, and successful traits of invaders. This dissertation research emphasizes community-related characteristics of successful invasions, bypassing the individual characteristics of invaders that may also make them successful in these

communities. In this fashion, my research fits into a much broader sub-field of invasive species ecology, and I attempt to draw in these complementary topics to place my work in its proper context.

Through the use of novel methods and robust datasets, my research pursues a broad understanding of the factors that affect exotic species success and their impacts on the communities they invade. My focal study systems are the plant communities of the southeastern United States, an ecological region with a rich history of academic study and contribution to the field of ecology (e.g. Odum 1969, Peet and Christensen 1980). I employed these systems due to their broad distribution across the landscape, the continued presence and success of exotic species within these systems, and their importance to biological diversity and conservation (e.g. Noss et al. 2015). Additionally, I utilized the data and methodology of a robust vegetation database, the Carolina Vegetation Survey (CVS). This database contains >6000 standardized plots assessing species presence and cover, woody stem distribution, and abiotic components of vegetation communities from across the southeastern United States (Peet et al. 1998, 2012). My work employs CVS methods and data to contribute additional knowledge to a general understanding of ecological communities throughout the region through the exploration of four key questions:

1. How does exotic species richness in plant communities vary with native species richness, and how does that pattern vary across environmental conditions and with spatial scale of observation?

2. What abiotic and biotic characteristics are significantly correlated with exotic plant presence in natural Southeastern communities, and how effective are these characteristics for predicting exotic species persistence?
3. Does exotic shrub invasion reflect pre-existing differences in local environmental conditions or affect changes in species richness metrics or structural components of forests?
4. How does experimental removal of invasive shrubs affect environmental conditions, such as temperature, light availability, soil moisture, and soil nutrient characteristics?

This research indicates generally that exotic species success is dictated by distinct processes and interactions depending on the scale of observation, as exotics are more prevalent in large-scale, species-rich plots than in their small-scale counterparts. Natural communities are assembled differently than expected by chance, and those sharing particular biogeographic and environmental conditions tend to express exotic species richness in differing yet somewhat predictable fashions. Several environmental characteristics correlate with exotic species success, including soil pH, calcium, woody stem density and cover of wetland species. The unique predictive ability of any individual variable remains limited, reflecting the complex interactions that drive exotic species success in these communities as well as the diversity of the exotic species involved. Once dominant, invasive plant species differentially affect invaded communities and must be considered in context, even those that are of similar structure, function and origin. Some dominant invaders, such as *Ligustrum sinense*, may foster losses in species richness and density of saplings and small trees, but also concurrent increases in vines and shrubs. By contrast, similar invaders may produce few

quantifiable effects on the communities they invade, such as with *Elaeagnus umbellata* invasion. Although shrub invasions, and the subsequent removal of dominant invaders, may cause demonstrable abiotic changes in the community, such as in temperature and light availability, responses in soil moisture and nutrient levels remain limited.

Some detected patterns of species invasions seem predictable and universal, though numerous other patterns of species invasions remain nuanced and context-specific. In this way, this research endeavors to add to the growing body of literature exploring these species and the communities they invade, in an effort to contribute to and broaden our understanding of associated ecological patterns and processes.

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CHAPTER 2: THE NATIVE-EXOTIC SPECIES RICHNESS RELATIONSHIP IN NATURAL COMMUNITIES VARIES WITH SPATIAL GRAIN OF MEASUREMENT AND ENVIRONMENTAL CONDITIONS

Introduction

Do communities with high species richness exhibit greater resistance to invasion by exotic species? Or, alternatively, do species-rich communities simply get richer? The hypothesis of community saturation suggests that diverse communities should be more resistant to the establishment of exotic species than their less diverse counterparts (Elton 1950). This concept, alternatively called the diversity-invasibility hypothesis, predicts that with increasing native species richness there will be fewer resources or niches available for exotic species to fill. Resident species can inhibit exotic species by reducing availability of limiting resources (Tilman 1999, Fargione et al. 2003), often by complementary use of resources (Fargione and Tilman 2005). As a consequence, resources are not readily available for exotic species to consume. By this same logic, given similar site conditions, less diverse communities might have higher availability of resources than their more diverse counterparts. In experimental studies, diversity has been shown to reduce community invasibility better than other measures, such as biomass (Hector et al. 2001, Tilman et al. 2001). Thus, according to this logic, exotic species should more readily establish in less diverse communities due to lower competition and greater access to resources (Case 1990, Stachowicz and Tilman 2005). The hypothesis can be extended beyond simple species richness to predict that species with niche characteristics that are poorly represented in the

regional flora can readily establish in suitable environments, particularly in communities with low richness (Gilbert and Lechowicz 2005).

Although many empirical and theoretical studies have supported the diversity-invasibility hypothesis as applied to plant communities, numerous others have reported contrary results (reviewed in Daleo et al. 2009)**.** Species richness values of exotic and native plants are often positively correlated in terrestrial communities (Meiners et al. 2002, Sax 2002, Tilman 2004, Stohlgren et al. 2006), particularly at large spatial grain (Brown and Peet 2003; Stohlgren et al. 1999, 2003, 2008). In general, high native-species richness predicts high exotic-species richness in plots of 1 m^2 or larger. By contrast, the diversity-invasibility hypothesis may prove more applicable at smaller spatial grains (i.e., smaller than 1 m^2). Such a pattern may be due to local biotic processes such as recruitment limitation (Seabloom et al. 2003, Sax et al. 2007, Stohlgren et al. 2008), neighborhood crowding (Kennedy et al. 2002, Brown and Peet 2003), and competition (Brown and Peet 2003, Huston 1999). Exotic species may successfully establish in communities of high native richness due to neutral sampling effects, whereby high native species richness predicts increased exotic richness by random establishment of new species (Herben et al. 2004). Exotic species establishment can also occur due to a similarity of resource demands between exotic and native species (Hierro et al. 2005) and increased local energy inputs and water availability (Albuquerque et al. 2011), as exotic species often succeed in areas of increased resource availability (Reichard and White 2001). The varying patterns of exotic species success at different spatial scales have introduced the concept of an "invasion paradox", the observation that multiple ecological processes may differentially impact diversity patterns at different spatial scales (Fridley et al. 2007).

Fridley et al. (2004) indicated that the paradox of scale associated with diversity-invasibility can be readily explained by comparison with a null model distribution. This null model randomly re-assigned species origins (i.e., exotic vs. native) within the regional species pool to determine if patterns of exotic richness are actually structured by species origin, or simply a random sample of species. Using 119 vegetated plots in the exotic-rich mountain riparian vegetation of the southern Appalachians, the authors demonstrated that the observed relationships of exotic species richness and native species were not significantly different from the predicted relationships of the permuted models. These results suggested that there is no evidence that exotic richness is influenced by species interactions or community assembly processes. A similar analysis of neutrally-assembled communities showed that the observed native-exotic richness relationships (NERR) reflected physical constraints on the number of individuals in a community, rather than community interactions (Herben et al. 2004).

It is important to determine whether community assembly dynamics structure exotic species establishment, or whether these patterns are no different from random expectation. This hypothesis is intrinsically hard to test because background species number is often a result of environmental factors that spatially covary with diversity (Brown and Peet 2003, Levine and D'Antonio 1999, Levine 2000, Foster et al. 2002), differences in habitat type (Stohlgren et al. 1999), or increased spatial heterogeneity at large scales (Davies et al. 2005, Kumar et al. 2006). In a large dataset that contains a wide range of plots, it is expected that these plots span many different types of environment conditions. Such environmentally heterogeneous data have the potential to display significant patterns in richness and

overcome a background signal of correlation with environment, due to the broad range of environmental predictors and resource types within the dataset (Fridley et al. 2007).

Here I explore three key questions:

1. How do exotic species richness patterns correlate with native species richness with changing spatial grain?
2. Is the Native-Exotic Richness Relationship (NERR) different from what would be expected by randomly assembled communities?
3. How does the NERR change due to changing environmental conditions?

To address these questions, I calculated the observed native and exotic species richness patterns in a dataset representing the range of natural vegetation across North and South Carolina. I subjected this empirical dataset to permutation tests to determine how the relationships between exotic richness and native richness compare to a null model of randomly assigned species origins. Finally, I subsetted this dataset to several vegetation community formation types in an effort to determine the predictive nature of exotic species presence with changing environmental conditions. This provided the opportunity to determine if, having incorporated broad ranges of environment and space to account for variation in null model applications, there is evidence that community processes shape exotic species establishment.

Methods

Study Region

My study spanned the region of North and South Carolina in the southeastern United States. This area covers 82,931 km^2, and extends from the coastal fringe, across the flatlands

of the Coastal Plain, the rolling hills of the Piedmont and reaches the highest peaks of the southern Appalachian Mountains with a maximum elevation of 2037m. (Figure 1). The region has a temperate climate and includes 523 community types recognized in the US National Vegetation Classification (NatureServe 2013). My analysis includes plots that represent 480 of these community types.

Plot Design and Selection

My analysis is based on 5022 plots from the Carolina Vegetation Survey database (Peet et al. 2012). These plots incorporate nested quadrats that record vascular plant species presence at multiple scales from 0.01 m^2 to 1000 m^2 (Peet et al. 1998). I extracted all plots from projects in North and South Carolina and removed any plots that re-sampled existing plots in the database. These data are representative of the geographic and compositional range of vascular plant communities of the Carolinas. Because many of the plots do not cover a full 1000 m^2, and because I wanted to include as many representative communities as possible, I included only 5 spatial grains for this analysis (0.01 m^2, 0.1 m^2, 1 m^2, 10 m^2, and 100 m^2).

Statistical Analysis and Null Model Development

To avoid spatial pseudoreplication, I randomly chose only one nested subplot from each available full plot of 100 m^2 or larger. I assigned species origins as native or exotic according to Weakley (2015). I developed generalized linear models of exotic richness as a function of native richness at each scale using the MASS package in R version 2.15.1 (R Core Team 2012). Due to the overdispersion of the species richness data, I modeled the data using a negative binomial error distribution.

I randomly re-assigned species origins in the entire dataset, keeping constant the total species richness in each plot and the frequency of exotic species throughout the entire region to ensure that random communities correspond to species distributions in empirical observations. I randomly re-assigned the origin of each species in the dataset in each permutation. I then re-tallied native and exotic species richness at each scale and calculated the slope of the generalized linear model between native and exotic species richness for each scale. I repeated this random re-assignment process 99 times for each empirical distribution to generate null distributions. I then repeated the random re-selection of subplots 99 times, for a total of 100 empirical slopes and 9900 null slopes. I calculated one-tailed *P* values to determine statistical significance, which represented the proportion of permutation-derived values that were as extreme or more extreme than the median empirical test statistic (Legendre and Legendre 2012).

Although previous research used this methodology (Fridley et al. 2004) to evaluate riparian community plots across a geographic span of 126 km and elevation gradient of 293 m, I analyzed a much larger dataset, encompassing many different community types in several physiographic regions and spanning 872 km in extent and 1903 m in elevational change. Additionally, the previous research had analyzed data with disproportionately high exotic species richness, relative to the general trends of the region. The application of this question and general methodology to a broader, more representative collection of species records enabled greater predictive ability for exotic species success.

Because neutral models predict exotic species richness to increase with increasing native species richness at large scales due to sampling effects, I also determined the percentage of species that were exotic in a plot as an additional measure of NERR. I

calculated the percentage of species in each plot that were exotic, fitting a linear model as a function of total species richness to determine how these percentages change with changing richness.

Constraints on the null model

Exotic species are significantly less frequent than native species throughout the examined communities (see Figure 2). A similar methodology re-assigned species origins within the regional species pool (Fridley et al. 2004). I replicated this re-assignment methodology in this analysis and determined that such re-assignment led to an artificial increase in exotic species presence throughout the permuted dataset and a biased result (Table 1). Therefore, I chose to constrain species re-assignments to species of similar frequencies across the dataset. This did not maintain an exactly similar distribution of exotic occurrences in the null datasets, but the result was relatively close. Because exotic species tend to be under-represented in natural datasets, relative to native species, random re-assignment of species origins inflates the percentage of species and individual occurrences that are "exotic". This leads to an inaccurate comparison community in the random permutation a requires constraints on the null model permutations. I considered an alternative method of permutation, namely changing the origin of individual occurrence records rather than species records. This approach would maintain the overall frequency of exotic organisms within the dataset and thereby yield more mathematically accurate results. This re-assignment strategy, however, is not representative of the biogeographic and community assembly patterns inherent in the dataset. Species are distributed throughout the region in general patterns due to their life histories and biogeographic methods of introduction. The strategy of individual permutations would disregard these significant and predictive

environmental patterns, reducing its practical application to natural communities, and thus was not used. Additionally, this re-assignment method did not significantly alter any of the results.

Comparison of Formations

Because the study region of the Carolinas within the southeastern United States contains a wide variety of environmental conditions, the NERR patterns vary among these unique conditions and differentially impact the overall trend of the NERR for the entire dataset. To determine how exotic species diversity varies in distribution across the study region, I subsetted the dataset according to broad assignments corresponding to environmental conditions. A useful subset is the formation assignment, as designated by the US National Vegetation Classification (Faber-Langendoen et al. 2014). Within the dataset of 5022 plots, seven formations contained at least 100 plots, representing three subclasses in the NVC hierarchy (Table 2). I performed independent empirical analyses for these formations, randomly selecting subplots to determine the generalized linear model of native and exotic richness at each spatial grain. I repeated the random selection of subplots 99 times, for a total of 100 empirical slopes for each region at each spatial grain.

Results

General Patterns

Across most scales, exotic richness is positively correlated with native richness (Table 3). At the very smallest scale examined, 0.01 m^2, exotic richness is negatively correlated with native richness. As spatial grain decreases, the slope of the NERR increases to 1 m^2, then decreases. As scale continues to decrease, however, the fixed space available for plant survival likewise decreases and can become a limiting factor of individual

abundance. As a result, species richness is affected by the fixed number of individuals capable of inhabiting a small subplot. Any high value of native species richness reflects a significant number of individuals in that space and thereby reduces space for exotic species, yielding a negative NERR. The slope at all grains is near zero, indicating that the frequency of exotics throughout the dataset is both much lower than native species and that exotic species are not inherently clumped at one extreme of species richness values within the dataset. This is corroborated by the change in percent exotic species with changes in richness (Figure 3). At scales >1 m^2, the slope of the best fit line is slightly positive, indicating that speciose communities tend to have a slightly greater share of exotic species. The slope is slightly negative at scales ≤1 m^2, indicating that species-poor plots have a slightly lower share of exotic species at those scales.

Comparison to null model

The slope of the NERR is significantly higher than the null model at the largest observed scale (100 m^2) (Table 3). The slope is significantly lower than the null model at the two smallest observed scales (0.1 and 0.01 m^2). Thus, although the communities generally exhibit a positive correlation between native and exotic richness, this relationship is not consistent relative to randomized distributions of species. At the largest scales, species-rich plots have more exotic species than one would expect by chance alone, while species-rich plots have fewer exotic species than expected at small scales. Indeed, the percentage of species that are exotic in the empirical plots increases with richness at spatial grains larger than 1 m^2 (Figure 3), indicating that exotic species are congregating in speciose plots more than expected by random community construction. By contrast, the percentage of species that

are exotic decreases with richness in the smallest communities, indicating limitations on local abundance and that interspecific competition may be affecting exotic species establishment.

Comparison of patterns within Formations

The median slope of the NERR for 100 random subsets differs among formation types across all scales (Table 4). For all but two formations, the NERR follows the general pattern with scale for the entire dataset, namely a positive and increasing relationship for 100, 10 and 1 m^2, a decreasing yet positive relationship at 0.1 m^2 and a negative relationship at 0.01 m^2. Warm temperate forests expressed essentially 0 slope at the largest spatial grain, decreasing to a negative relationship at 1 m^2 and smaller. By contrast, temperate freshwater marshes, wet meadows and shrublands expressed a positive relationship at all spatial grains, though the relationship is near zero at 0.01 m^2, which may reflect the very low diversity of these systems.

Discussion

General patterns

The positive correlation between native and exotic species richness at most empirical scales supports previous findings (e.g. Stohlgren et al. 2008). The increasing percentage of exotic species in large-scale, speciose plots also corroborates other analyses (e.g. Albuquerque et al. 2011), though the magnitude of this change is not as strong as has been reported elsewhere. This suggests that different processes influence species richness at different scales. Where spatial grain is $\geq$ 1 m^2 greater heterogeneity can be expected, which provides increased opportunities for species establishment and a positive NERR. At the smallest scale, however, the NERR and slope of percent exotics is negative, indicating that

species-rich plots have fewer exotic species than species-poor plots of the same size. This corroborates and expands on conclusions of previous research, and suggests that spatially-structured interspecific competitive exclusion may limit the available space for exotic establishment at very small scales (e.g. Brown and Peet 2003; Kennedy et al. 2002).

The species richness patterns observed by this analysis likely reflect other, more predictive patterns and processes within the observed communities. Such underlying processes may provide valuable information for invasive species management and prevention. Relationships between native and exotic richness are arguably less a result of diversity itself than of environmental factors that spatially covary with diversity (Levine and D'Antonio 1999; Levine 2000; Foster et al. 2002). Resource availability, whether reflecting unused nutrients in the community or disturbance processes, is an important component of establishment of any exotic species. Species richness patterns respond inconsistently to changes along a productivity gradient (e.g. Grime 1973, Huston 1979, Adler et al. 2011; reviewed in Peet et al. 2014). There is some evidence, however, that resource availability and other abiotic environmental characteristics, in concert with species richness patterns, can predict sites with high potential for potential exotic species establishment (Catford et al. 2011). Where environmental data may be challenging to collect and compare, this analysis demonstrates that native species richness patterns may provide an adequate predictor for exotic species establishment. While exotic species establishment can vary dramatically with native species richness among environmental conditions (for example, the speciose yet exotic-poor *Pinus palustris* savannas), general predictive patterns emerged for the majority of community formations tested here.

Increased spatial grain inherently leads to increased spatial and environmental heterogeneity (Davies et al. 2005, Kumar et al. 2006), suggesting that larger scales should exhibit higher species richness values and positive NERR. Spatial heterogeneity also reflects differences in response with habitat type (Stohlgren et al. 1999), owing to the fact that different habitats and communities are differentially susceptible to exotic species invasions (Kalusová et al. 2013). Finally, the available species pools of both native and exotic species significantly impact community richness patterns across all observed spatial grains (Morueta-Holme et al. 2013). These local species pools vary with multiple factors, including geography, proximity to human activity, and environmental conditions. As such, pools of available species vary among community formation types, which may further explain the differences in exotic species establishment in different habitats.

Comparison to null model

Contrary to previous findings (e.g. Fridley et al. 2004), the empirical NERR is significantly different from the permuted relationships across most scales. At small scales, the observed slope of the regression line is lower than expected from the null model, suggesting that exotic species may be inhibited from successfully establishing in species-rich communities. Conversely, species-poor communities may have higher susceptibility to invasion, thus driving the slope down relative to those exhibited by random distributions. These findings indicate that limitations on space and interspecific competition are likely affecting the potential species richness, as demonstrated by Herben et al. (2004). Any high value of native species richness reflects a significant number of individuals in that space and thereby reduces space for exotic species, depressing the NERR. In either case, exotic species establishment is lower in species-rich communities than would be suggested by the randomly

assembled communities from the same regional species pool. At large spatial grain, the opposite pattern is expressed; exotic species are more prevalent in species-rich communities than expected by chance. These two results, taken together, indicate that the community assembly processes dictating exotic species establishment vary in their impact with varying scale, consistent with species richness patterns in plant communities (Shmida and Wilson 1985). Large-scale community interactions, such as propagule pressure and disturbance patterns, may favor exotic species more than expected by chance (Davies et al. 2005), while small-scale interactions, such as plant-on-plant competition (Wilson and Tilman 1993) typically reflect a lower exotic presence. These findings corroborate the major tenants of the invasion paradox (Fridley et al. 2007). A similar randomization approach to species richness patterns across a 1 km^2 grid in an urban landscape showed lower than expected exotic richness on species-rich sites. However, that result derived from observations at a scale where niche process are unlikely to operate and instead likely resulted from aliens having different environmental requirements than natives (Ricotta et al. 2010). That study did reinforce the importance of null model tools in determining important community patterns.

Previous empirical efforts examining the NERR have failed to resolve whether native species richness is an adequate predictor of exotic richness, or whether it is simply a correlate that spatially covaries with exotic species richness. My work presents a broad, general analysis across many resource regimes, physiographic regions and community types in an effort to detect and explain general patterns of exotic species establishment across heterogeneous environments. Although I am not able to conclude that the observed patterns are exclusively attributable to community assembly processes and species interactions, these

results indicate that such processes are occurring, although likely in concert with numerous abiotic and spatial phenomena that influence species richness.

Sessile organisms, such as plants, require a caveat in application of the diversity-invasibility hypothesis. Given that these organisms cannot move to directly out-compete all those beyond their immediate competitive neighborhood, coexistence can occur among a multitude of small-scale species combinations, even if they utilize the same resources. The carousel model (van der Maarel and Sykes 1993) explains how individuals of different species may overlap in their growing locations within a community such that they utilize the same resources while multiple species persist. Such is the case if inferior competitors have sufficiently high dispersal rates to locate and colonize sites not already occupied by superior competitors (Tilman 1994), as suggested by the persistence of "waif" species in long-term vegetation dynamics (Grime 1973). Changes in temporal scale (Clark et al. 2013) or disturbance pattern (Belole et al. 2008) may also impact native-exotic diversity patterns. Thus, single-sample plots may not adequately reflect the many discernable biotic and abiotic patterns contained in plant communities. Likewise, the assemblage of species identities and their unique life strategies, rather than species richness, may prove more suitable predictors of invasibility by exotic species (Crawley et al. 1999). Species traits are often linked more directly to ecosystem functioning and productivity than metrics of species richness (Tilman et al. 1997) and may better predict biodiversity patterns. Such considerations may provide worthwhile future extensions of this work.

Comparison of Formations

The patterns of change in NERR with scale, for both the entire dataset and for most of the study regions, are consistent with previous findings (Fridley et al. 2007). These results

indicate that for most communities throughout the southeastern United States, exotic species establishment may prove somewhat predictable, given the unique environmental, biogeographic and spatial contributors of species richness. It may be expected across the majority of communities that NERR is positive and slightly increasing up to moderate spatial grains, below which individual competitive effects dictate, and limit, exotic species success due to priority effects. These patterns are not universal, however, though deviations in such patterns may prove predictable, given specific environmental conditions.

Warm temperate forests and woodlands (largely longleaf pine savannas), which expressed relatively low NERR at all scales and negative NERR at most scales, contain communities that are among the most speciose, yet-exotic poor in the entire study region. Although the NERR is positive at the largest spatial grain for these formations, this is likely reflective of simple sampling effects due to spatial heterogeneity (Herben et al. 2004). The interspecific competition for space and resources in small-scale, speciose communities, coupled with priority effects, indicates that exotic species seem to be only successful in locations devoid of such high competition, as evidenced by a drastic reduction in species richness in these plots when exotic species are present (Table 2). By contrast, the positive NERR across scales in temperate freshwater marshes, wet meadows and shrublands suggests disparate resource availability patterns among plots in this formation. As a result, exotic species tend to be clumped in distribution in these plots, likely succeeding in more favorable resource conditions in the same manner as native species. Such patterns are particularly evident in the case of this formation, where intermittent soil flooding and saltwater intrusions can filter the regional species pool more dramatically than most other formations in the study region (Flynn et al. 1995). This is evidenced by the significant increase in species richness in

these plots when exotic species are present, a stark contrast to the patterns detected in the warm temperate forests. The variation in species and resource distributions is inconsistent for communities within each of these unique formations, so these results may prove predictive of exotic species establishment based on resource, heterogeneity and species distribution data for other temperate vegetation formations.

Conclusion

Although many abiotic and spatial factors can influence exotic species establishment and richness in vegetated communities, this analysis examines simultaneously many environmental conditions and community types in an attempt to overcome unique biogeographic and abiotic predictors that may confound local empirical analyses. The results suggest that exotic species establishment is dictated by distinct processes and interactions, depending on the scale of observation as exotics are more prevalent in large-scale, species-rich plots than in their small-scale counterparts. Similarly, communities sharing unique biogeographic and environmental conditions tend to express exotic species richness in differing and somewhat predictable fashions. I conclude that community assembly processes, species richness patterns, and species interactions all significantly impact the potential for invasion across a broad range of terrestrial plant communities.

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Tables and Figures

Table 1. The frequency of species origins within the empirical dataset, permutation of species records, and constrained permutation. Due to the under-representation of exotic species, permutation of species records artificially inflates exotic species frequency in the permuted dataset. This bias was much less apparent when permutations were constrained to within small ranges of similarly frequent species in the dataset.

Assigned Origin	Frequency in Empirical Dataset	Median Frequency in Original Null Dataset	Median Frequency in Updated Null Dataset	Percent of Empirical Dataset	Median Percent in Original Null Dataset	Median Percent of Updated Null Dataset
Exotic	3374	6279	3976	2.46	4.7	2.9
Native	130714	122087	129780	95.44	92.2	94.76
Unknown	2870	4121	3202	2.1	3.1	2.34

Table 2. Comparison of exotic species distributions among the seven most common community types of the Carolinas, as assigned by the US National Vegetation Classification level of "formation". The frequency of exotic species differs significantly among community types.

Formation Type	Number of Plots	Percent Exotic Occurrences	Percent Exotic Species	Mean Richness of All Plots	Mean Richness of Plots with Exotics
Entire Dataset	5022	1.72	8.12	53.40	58.67
2.B.4:Temperate Scrub and Herb Coastal Vegetation	216	2.72	7.69	22.43	20.95
1.B.2:Cool Temperate Forest and Woodland	1665	1.24	6.94	62.99	67.26
2.B.2:Temperate Grassland and Shrubland	128	2.89	4.89	38.09	33.98
2.C.4: Temperate Freshwater Marsh, Wet Meadow and Shrubland	452	3.02	7.28	44.50	65.12
1.B.1: Warm Temperate Forest and Woodland	796	0.68	4.24	64.34	48.43
1.B.3: Temperate Flooded and Swamp Forest	1225	3.69	8.14	55.19	68.38
2.C.5: Salt Marsh	248	1.15	2.92	22.08	16.88

Table 3. Comparison of observed and permuted species richness relationships for the entire dataset. Across most scales, the NERR is positive in both the observed and permuted communities, whereas this relationship is negative at the smallest observed scale (0.01 m^2). At larger scales (100 m^2), the observed relationship's slope (s) is significantly higher than the null model, but is significantly lower than the null model at smaller scales (0.1 and 0.01 m^2).

		Observed Relationship (100 Random Subsets)			Null Relationship (99 Re-assignments of each random subset; 9900 slopes total)					Median Observed vs. null (p-value)
Scale (m^2)	N	Min Slope	Median Slope	Maximum Slope	Min Slope	5% Slope	Median Slope	95% Slope	Maximum Slope	
100	5022	0.0426	0.0436	0.0442	0.0199	0.0228	0.0286	0.0359	0.0441	0.005^
10	4966	0.0595	0.0641	0.0673	0.0234	0.0351	0.0532	0.0699	0.0746	NS
1	4954	0.0627	0.0741	0.0849	0.0463	0.0567	0.0849	0.119	0.130	NS
0.1	4864	0.0158	0.0413	0.0674	0.0478	0.0688	0.129	0.181	0.212	0.001**
0.01	4383	-0.710	-0.560	-0.398	-0.361	-0.348	-0.204	-0.026	-0.012	0.001**

** $p<0.001$ at lowest tail; * $p<0.05$ at lowest tail; ^^$p<0.001$ at highest tail; ^$p<0.05$ at highest tail

Table 4. The median slope of the NERR for 100 random subsets differs among formation types across all scales. For all but two formations, the NERR follows the general pattern with scale for the entire dataset, namely a positive and increasing relationship for 100, 10 and 1 m^2, and a decreasing yet positive relationship at 0.1 m^2 and a negative relationship at 0.01 m^2. Warm temperate forests expressed essentially 0 slope at the largest spatial grain, decreasing to a negative relationship at 1 m^2 and smaller. By contrast, temperate freshwater marshes, wet meadows and shrublands expressed a positive relationship at all spatial grains, though the relationship is near zero at 0.01 m^2.

Formation Type	100 m^2	10 m^2	1 m^2	0.1 m^2	0.01 m^2
Entire Dataset	0.044	0.064	0.074	0.041	-0.56
2.B.4:Temperate Scrub and Herb Coastal Vegetation	0.011	0.049	0.072	0.038	-0.075
1.B.2:Cool Temperate Forest and Woodland	0.027	0.056	0.134	0.092	-0.32
2.B.2:Temperate Grassland and Shrubland	0.015	0.034	0.194	0.061	-0.05
2.C.4: Temperate Freshwater Marsh, Wet Meadow and Shrubland	0.011	0.047	0.109	0.052	0.01
1.B.1: Warm Temperate Forest and Woodland	0.011	0.002	-0.025	-0.10	-0.81
1.B.3: Temperate Flooded and Swamp Forest	0.015	0.050	0.104	0.039	-0.64
2.C.5: Salt Marsh	0.051	0.093	0.365	0.092	-0.04

Figure 1. Map of study region, centered on North and South Carolina, southeastern United States. Each dot represents one sampled location, totaling 5022 analyzed plots.

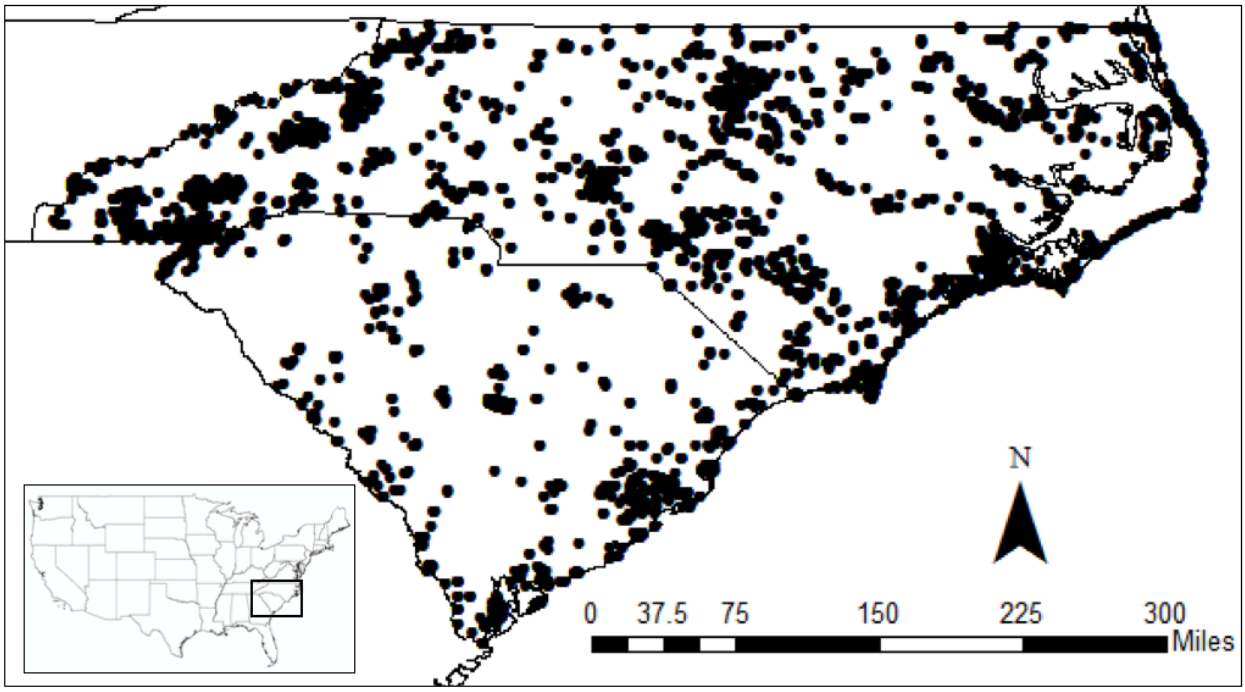


Figure 2. Species occurrences in the dataset and individual plots. Exotic species are much less frequent than native species (a) throughout the entire dataset (median frequency: exotics=3 occurrences; natives=9 occurrences) and (b) in individual plots (median frequency: exotics=0 occurrences; natives=25 occurrences).

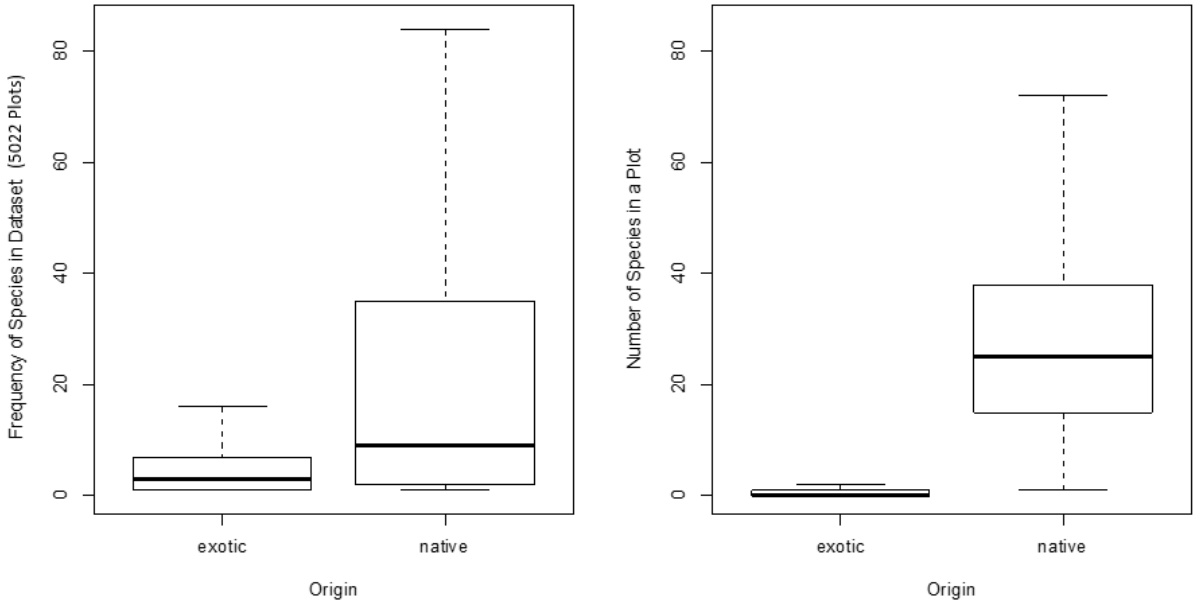
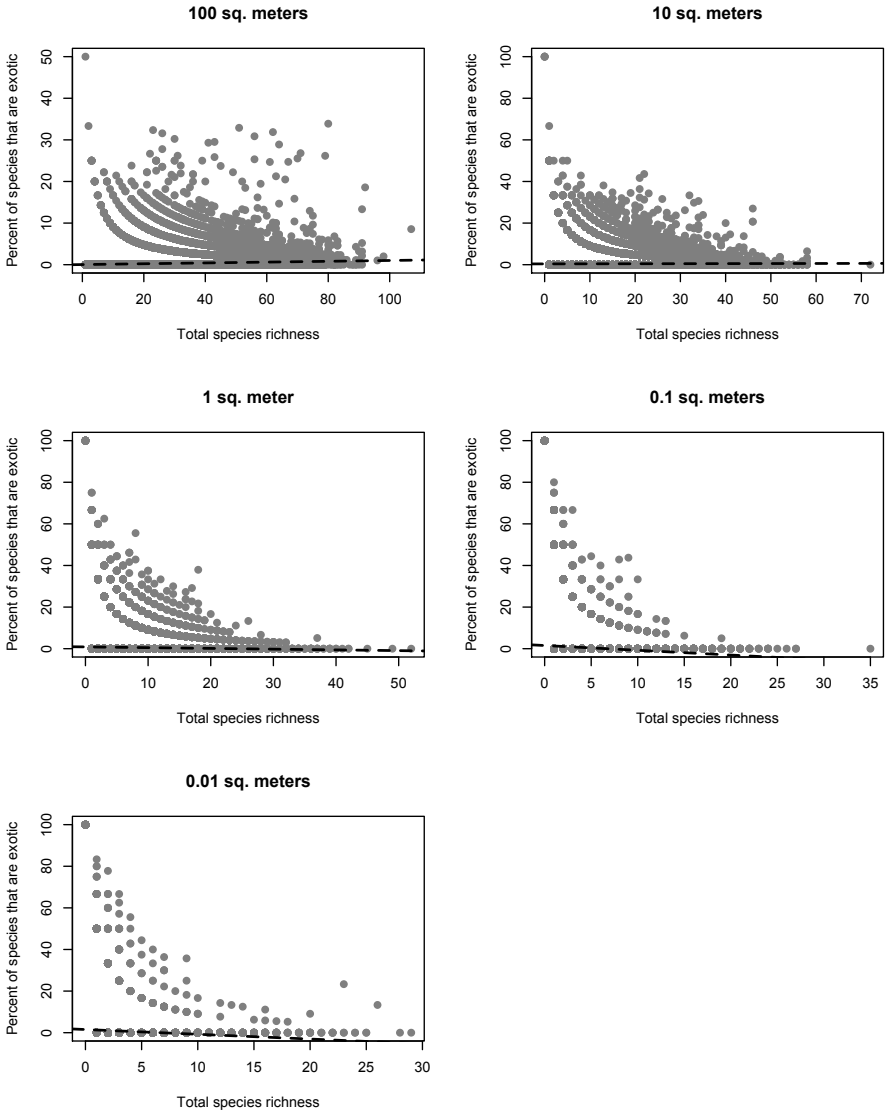


Figure 3. The percentage of species at each spatial grain that are exotic, as a function of total richness of the subplot. At scales >1 m^2, the slope of the best fit line is slightly positive, indicating that speciose communities tend to have a greater share of exotic species. The slope is slightly negative at scales ≤1 m^2, indicating that species-poor plots have a greater share of exotic species at those scales.



CHAPTER 3: EXOTIC SPECIES SUCCESS IS CORRELATED WITH MANY ENVIRONMENTAL CHARACTERISTICS IN SOUTHEASTERN U.S. PLANT COMMUNITIES

Introduction

Exotic species represent a critical concern for conservation and land management practices around the globe (Bellard et al. 2016). Exotic species are considered established in novel environments when viable reproductive populations persist beyond initial colonization (Rejmánek et al. 2013). Once exotic species have established, resources needed for management and removal dramatically increase. Thus, it is imperative that the factors that contribute to their establishment be well understood. Although many studies have examined environmental and biotic factors associated with the successful persistence of exotic species (hereafter, ESS for "exotic species success"; e.g. Catford et al. 2009), general predictions remain elusive.

Factors and conditions associated with topography and human influence may best predict establishment, such as the amount of propagule pressure due to road and stream proximity (D'Antonio et al. 2001, Anderson et al. 2013, Greene and Blossey 2014). Additionally, ESS is often correlated with land-use history (Lundgren et al. 2004) or changes in local disturbance regimes (Nagler et al. 2005). Such disturbances may yield fluctuations in soil nutrient availability, creating novel opportunities for successful establishment when associated with timely introduction events (Theoharides and Dukes 2007). Similarly, disturbances may increase light and moisture resources availability (Davis and Pelsor 2001),

resulting in changes that favor exotic species (Catford et al. 2011). These responses are not universal, however, as exotic species successfully establish across a wide variety of resource regimes (Mostoller 2008, Foard 2014) and maintain their competitive advantages over native species in a variety of physiological conditions (Heberling and Fridley 2016).

Unfortunately, much previous research investigating environmental correlates of ESS has analyzed a single exotic species or similar functional groups, reducing the general applications of the research. Though some broad analyses have examined the shared traits and roles exotic species play in communities (e.g. Pyšek and Chytrý 2014, van Kleunen et al. 2014), there is mixed support for many hypotheses concerning predictors of successful establishment and invasion (Catford et al. 2009).

Here I explore two key questions:

1. What abiotic and biotic characteristics are significantly correlated with exotic plant cover in natural southeastern U.S. plant communities?
2. How effective are these characteristics for predicting successful persistence of exotic plant species?

Many exotic species are introduced intentionally for horticultural purposes, primarily in environments with high resource and moisture levels (Reichard and White 2001). For this reasons, I predicted ESS to be positively correlated with key soil nutrient characteristics, such as nitrogen, potassium and phosphorus, and with proxies of community moisture availability, such as the total cover of wetland species and slope. However, due to the inconsistent introduction and success of exotic species within the landscape, I predicted that these correlations would not yield robust predictions of ESS when used in concert.

I analyzed a dataset of 1038 vegetation plots across a broad physiographic region, with a suite of >200 exotic species present, for environmental correlates shared among plots experiencing ESS. In this way, I determined shared environmental conditions of communities impacted by exotic species in an effort to develop increased predictive ability across a large geographic range.

Methods

Data Collection and Selection

To examine the abiotic and biotic predictors of exotic species success (ESS), I identified and calculated 27 unique environmental variables potentially associated with ESS (see Table 1 for a description of each predictor used in this manuscript). I extracted species records and environmental data from the Carolina Vegetation Survey database (Peet et al. 2012) that conform to the CVS protocol (Peet et al. 1998). This database currently contains >6000 such vegetation plots across the southeastern United States. CVS methodology identifies all vascular plant species within the plot for up to six different spatial grains and measures all stems that reach breast height (Figure 1). Individual species cover was assessed at time of data collection on a visual scale (Table 2). CVS protocol measures several geographic and topographic features of the sampled communities, such as elevation, slope, aspect, and median soil depth, though some measurements are not universally collected among plots. Finally, many CVS plots include soil nutrient, texture and bulk density measurements from soil samples taken from the top 10 cm of the soil profile. For this analysis, I extracted from this dataset all uniquely sampled and standardized CVS plots in North and South Carolina that were ≥400 m^2 in area, assigned a location in the Piedmont physiographic region, and included both species cover values and soil data. Plots greater

than 400 m^2 were constrained to that size for consistency of analysis, typically by including only the four intensive modules sampled in standardized CVS protocol. I chose the Piedmont physiographic region because of its robust number of sampled plots within the dataset, the consistency of environmental data collected for each plot, the broad environmental conditions spanning its range, and the many exotic species that occur in plots from this region. This collection resulted in a dataset of 1038 plots for this analysis (Figure 2).

Soil samples were collected from the top 10 cm of the mineral soil profile in each plot upon initial data collection. Soils were dried at ~50^0 C for ~48 hours, sieved, weighed, and shipped to Brookside Laboratories Inc. Nutrient analyses employed the Mehlich III method (Mehlich 1984). Total cation exchange capacity (meq/100g), pH, estimated nitrogen release, easily extractable P, exchangeable cations (Ca, Mg, K, Na ppm), percent base saturation, soluble sulfur and bulk density values were determined for a composite sample of the four subsamples from each plot. Some plots include soil data for multiple individual subplots; for these cases I calculated the median value of each soil characteristic for each plot.

I performed post-sampling calculations to quantify several topographic and biotic variables of interest in predicting ESS. I calculated each plot's straight-line distance to the nearest stream in ArcMap (9.3.1), using the EPA National Hydrography Dataset Plus stream data (region 03N). I calculated each plot's straight-line distance to the nearest road centerline in the study region, using state DOT maps of primary and secondary roads in North and South Carolina. These maps depicted all public roads with at least one lane of traffic in each direction, thereby serving as a common corridor for vehicle movement. Plots with geolocation uncertainty >200 m or a measured distance to either road or stream >4000 m were omitted from this analysis, resulting in 840 plots analyzed for proximity measures.

Using CVS species records, I calculated the total native species richness of each plot at 400 m^2, as well as the single native species of greatest cover for each plot. If plots contained multiple species at the greatest recorded cover level, those plots were not included for analyses considering a dominant native, in an effort to reduce the confounding relationships of co-dominant species within communities. Instead, only those with unique dominant native species were included, resulting in 887 plots for analysis using that categorical variable. Using stem records, I calculated the canopy basal area and stem density for each plot. Finally, because soil moisture may be a suitable predictor of exotic species success but is not measured in CVS protocols, I used species records to calculate a proxy measure for plot moisture and wetness. For this purpose, I calculated the total visual cover of species in each plot that are listed as obligate wetland or facultative wetland species according to the 2014 National Wetland Plant List (Lichvar et al. 2016). I tested each continuous predictor variable for normality of distribution, and transformed non-normal distributions as needed, such as aspect and soil nutrient content (see table 1 for transformations). I then standardized each variable individually, such that the mean measured value for each variable was converted to zero. All values for that variable were likewise converted to their corresponding z score to demonstrate the deviation of variables with ESS, for more uniform comparison of impacts between variables.

I calculated several continuous and binary metrics of exotic species success for each plot. First, I summed the total cover of species considered "exotic" to the southeastern United States, according to Weakley (2015). Cover values were assigned as the geometric means of the percentage cover for that cover class (Table 2), as species occurrences tend to occur disproportionately in the lower portion of each cover class (Peet and Roberts 2013).

All exotic species cover means were summed for each plot. Because "exotic species success" may vary with environment and community type, I binned the plots according to their exotic cover using several thresholds of success: 1% total cover, 2% total cover, 5% total cover, 10% total cover and 20% total cover. Plots reaching or exceeding these thresholds were assigned a binary "invaded" distinction in the dataset, and the continuous value of exotic cover was maintained for future analysis. For this analysis of 1038 plots, 210 plots expressed >1% exotic cover, 152 plots expressed >2% exotic cover, 89 plots expressed >5% exotic cover, 52 plots expressed >10% exotic cover and 21 plots expressed >20% exotic cover. For most analyses, "exotic species success" (ESS) is considered as at least 5% cover of exotic species in the plot. Finally, several unique exotic species are frequent enough within the dataset to warrant analysis of these predictor variables individually. I partitioned the dataset for each of the most frequent exotic species within it, assigning plots with that species present as "invaded" and those without that species as "uninvaded" for each species (see Table 3).

Data Analysis

To determine which abiotic and biotic variables correlate with ESS, I performed binomial regressions of each continuous variable with each success threshold using the MASS package in R version 2.15.1 (R Core Team 2012), for a total of 125 binary models. Plots meeting the threshold for exotic cover were designated with a "1" at the given threshold, while all other plots were designated with a "0". I calculated the slope of the binomial regression line and the Wald test statistic to determine significance of each model (Legendre and Legendre 2012). Because data and soil collection were not consistent across all plots, some regressions were performed on as few as 298 plots, while others were

performed on 1038 plots. The four variables most significantly correlated with ESS were maintained for future analyses, so as to maintain as many plots for analysis as possible without losing significant predictive data. I performed a principal components analysis of all soil and topographic characteristics in R, and determined the predictive ability of the first axis of variation regarding ESS, as well as its correlation with individual predictor variables.

Using the four most significant variables for a total of 640 plots, I developed a generalized linear mixed-effects model of total exotic species cover in each plot using package lme4 in R, using a residual maximum likelihood distribution for less biased predictions. The random effect for the model was the categorical variable corresponding to native species of greatest cover for each plot, which assumed that there exist underlying differences in ESS patterns across the region corresponding to this categorical variable. Communities dominated by different species would correlate to ESS in non-predictable fashions from one another. The fixed effects in the model were the four significant continuous variables, which assumed the patterns of ESS in the dataset corresponded with numerical differences in those variables. I determined the variance attributable to the categorical variable and residual variance in the model. I also projected the predicted model data back onto the original distribution to determine a correlation value of the mixed effects model fit to the data. I calculated the relative importance of each retained variable in predicting exotic cover using the LMG (Lindeman, Meranda, and Gold) method, an unweighted decomposition of the total R^2 for each individual variable, in the relaimpo package in R (see Grömping 2006 for a review). I then developed a classification and regression tree to partition plots according to these significant variables with the tree package in R. Plots with at least 5% cover of exotic species were designated with a "1" and all others

were designated with a "0". I then individually re-analyzed the predictor variables for correlation with exotic species presence in the dataset for each of the most frequent exotic species (Table 3).

Results

Of the 26 continuous variables analyzed via binomial regression, 13 are significantly correlated with exotic species success (ESS) at each of the four thresholds (Table 4). Most significant soil nutrient measures, including calcium, magnesium, pH, sodium, exchange capacity and base saturation, demonstrate a positive relationship with ESS. Several soil properties, however, such as bulk density and sulfur, express a significantly negative relationship. Significant biotic measures, including wetland species cover, basal area and stem density demonstrate positive relationships with ESS. Finally, significant topographic measures, including slope and elevation, express negative relationships with ESS. All measures of soil texture and proximity to roads or streams are non-significant across thresholds of ESS. The four variables most significantly correlated with ESS, regardless of threshold of exotic species cover, are soil pH, calcium, stem density, and the cover of wetland species.

The dataset is represented by a wide variety of dominant native species within plots and a corresponding variation in exotic species cover among plots dominated by different native species (Figure 3). Plots dominated by typically xeric species, such as *Quercus spp.* (oaks) and *Carya spp.* (hickories), tend to have little exotic cover, as represented by the open data points. By contrast, plots dominated by mesic species, such as *Acer spp.* (maples) and *Liquidambar styraciflua* (sweetgum), typically have greater exotic cover, as represented by closed data points. This pattern holds across thresholds of exotic species cover and for the

most frequent exotic species in the dataset. Although these individual dominant species may seem indicative of broader patterns, the predictive ability of the categorical variable "native species of greatest cover" remained quite low in the mixed effects model (value of 2.565; residual variance of model of 43.622). In all, the data fitted using the mixed effects model correlated to the observed data at a rate of 0.2398.

Much like native species of greatest cover, significant continuous variables tend to have low predictive importance in the model (Figure 4a). Altogether, the four most significant variables predict 10.8% of the total variation in exotic species cover, led by the cover of wetland species (4.8%), then stem density (2.9%), calcium (1.6%), and pH (1.5%). Incorporating the 10 most significant variables does not greatly influence the model's fit (Figure 4b). Thus, a significant amount of variation in ESS remains unexplained by these models. Finally, the classification and regression tree analysis indicates that many environmental conditions can be used to explain where establishment is unlikely to occur (Figure 5). In this analysis, the tree output includes the average ESS value for plots exhibiting each unique suite of environmental conditions. Plots with <5% cover of exotic species, represented in the tree as a value of "0", were consistently similar in environmental conditions. This is indicated by the broad suites of conditions that express values approaching 0, meaning that the vast majority of plots in that group were uninvaded. However, few suites of environmental predictors can readily predict ESS, as evidenced by the few numbers approaching 1 in the analysis. Plots that are experiencing ESS are not explicitly different in environmental conditions from non-affected plots. Where ESS can be determined across the dataset, wetland species cover seems most effective in distinguishing sites with ESS.

The principal components analysis indicates that, as with the classification and regression tree, it is easier to predict where exotic species do not occur than to distinguish where they do (Figure 6). No principal component readily predicts ESS, though a combination of wetland species cover and sodium content seems most correlated with plots containing exotic species.

Of the 27 continuous variables in this analysis, each focal exotic species is significantly correlated with between 5 and 22 of the variables (Table 5). The direction of correlation of most environmental characteristics is consistent, though not universal, among species. For example, ESS is positively correlated with base saturation, calcium, magnesium, native species richness, pH and stem density, and negatively correlated with elevation and distance to road and stream, for all focal exotic species. By contrast, the correlation of ESS with both sulfur and cover of wetland species was consistent for all species except *Celastrus orbiculatus.* The most frequent species tend to have more significant correlations than those that are less frequent in the dataset, though the magnitude often varies with species. As with exotic species cover in the entire dataset, the most significantly correlated variables, regardless of the focal species, tend to be basal area, calcium, elevation, magnesium, pH, stem density, and wetland cover.

Discussion

Exotic plants often survive and establish more effectively in riparian areas than comparable upland sites, due to greater propagule pressure, nutrient availability and soil moisture (Matthews et al. 2011). In particular, propagule pressure is one of the strongest predictors of ESS across systems (D'Antonio et al. 2001, Brown and Peet 2003, Catford et al. 2011) Additional characteristics of riparian areas, such as low slope, high soil moisture and

greater stem density, similarly correlate with successful establishment, providing a confluence of related factors that enable exotic species to succeed in novel environments (Taylor et al. 2015). Although aspect may be an effective predictor of vegetation change in some systems (Bennie et al. 2006), the suite of exotic species of the Piedmont likely favors other topographic features more than they do orientation towards the sun, particularly in flat riparian areas. A lack of correlation between soil texture and ESS indicates that exotic plants in the southeastern Piedmont are capable of surviving across a range of soil types, as evidenced by their continued success in a variety of environments (Mostoller 2008, Heberling and Fridley 2016). In many regions, exotic species may prove better adapted than their native competitors to novel disturbance regimes and changes to local environmental conditions (Oduor et al. 2016), a competitive advantage that facilitates ESS in such communities.

The positive relationship between ESS and most significant soil nutrient characteristics suggests that exotic species succeed most often in fertile sites, consistent with my initial hypothesis. Particularly in fertile sites high in other necessary resources, calcium can serve as a limiting resource for plant growth (Banath et al. 1966). This likely causes the strong positive correlation between ESS and calcium in these communties. Magnesium is a micronutrient with important roles in plant growth, particularly the development and function of cellular proteins and enzymes, and is strongly correlated with soil fertility (Brady and Weil 2007). Increases in pH, exchange capacity and base saturation generally reflect the improvement of overall soil fertility in this geographic range. In the heavy clay soils of the Piedmont, the negative relationship of ESS with bulk density likely reflects an increase in exotic species with increased porosity and drainage.

The positive correlation of ESS with biotic measures, such as wetland species cover, basal area and stem density, may be expected in ecological systems. A similarity of resource demands between exotic and native species (Hierro et al. 2005), or neutral sampling effects (Herben et al. 2004), may explain exotic species success in areas with successful natives. Such relationships can occur due to spatial factors that co-vary with diversity (Foster et al. 2002), including spatial heterogeneity or gap dynamics that may drive species establishment and success. Native-exotic richness patterns are not universally positive, however, as some evidence indicates that species with niche characteristics that are poorly represented in the regional flora can readily establish in environments of low native richness or productivity (Gilbert and Lechowicz 2005). Indeed, native and exotic species often co-exist without significant competitive interactions (Davis et al. 2015), as is demonstrated by several of the focal exotic species in this study. For example, *Microstegium vimineum* is a shade-tolerant C_4 grass with the potential to succeed in a wide variety of environmental conditions (Anderson et al. 2014). Beyond the ample understory of Piedmont forests, low nitrogen levels in the soil may facilitate exotic C_4 grasses, which are poorly represented in the native flora of the southeast. Similarly, *Celastrus orbiculatus* prefers open woodlands, but has demonstrated shade-tolerant capabilities and increased success on steep slopes compared to its native congeners (Ellsworth et al. 2004).

The lack of predictive ability of the generalized mixed-effects model suggests that although dominant native species may give clues as to potential for exotic species persistence, even these factors do not readily explain the complex interactions of biogeographical, anthropogenic and life history patterns of both the communities and the exotic species being studied. A significant predictive component of ESS not included in this

analysis is human influence (Chytrý et al. 2008, Catford et al. 2011), as ESS is often correlated with land-use history (Lundgren et al. 2004) or changes in local disturbance regimes (Nagler et al. 2005). These features are captured to some extent through several related characteristics, such as the dominant native species and the proximity to roads. For example, the late-successional oak and hickory forests of the Piedmont are less likely to have been disturbed or experienced succession in recent decades than sites dominated by generalist maple and sweetgum species (Abrams 1998), thereby reducing potential opportunities for exotic species. While such findings seem logical, the limited predictive ability of these characteristics to ESS may suggest further analyses of anthropogenic effects are warranted.

A significant amount of variation in species distribution patterns remains unexplained by single variables, consistent with explorations of community patterns throughout the region (Coyle and Hurlbert 2016). The values of groupings in the classification and regression tree indicate that while there are multiple environmental conditions where exotic species do not currently establish (represented by values near 0), very few conditions exist in which exotic species consistently establish (represented by values near 1). Plots with ESS conditions match many sites with similar conditions that did not experience ESS at the time of sampling. These results may suggest that ESS is not uniform across landscapes, even within a well-defined physiographic region, and is reflective of additional interactions not here considered. The inconsistent predictive ability of ESS may instead reflect incomplete establishment of exotic species across the study area, either through lack of propagules or inconsistent disturbance patterns. It is probable, therefore, that ESS will continue throughout these communities with increased human exposure and persistent propagule pressure (Catford et al.

2011). Patterns of ESS will likely be magnified and expanded, even in well-established regions, through further globalization (Callen and Miller 2015, Amano et al. 2016) and as a consequence of future global climate change (Leishman and Gallagher 2015). This is particularly the case throughout the forests of the Eastern United States, as human modification of the forest continues to make sites more suitable for ESS, particularly through continued fire suppression and promotion of mesic communities in management practices (Nowacki and Abrams 2008).

Ecological communities are not static pools that simply allow exotic species to enter and persist or prevent them entirely. Rather, the plots utilized in this analysis are a single representation in time of the dynamic interactions between native and exotic species and their surroundings. Exotic species may not be documented in a plot at the time of sampling, even in what would otherwise be ideal conditions, for a variety of reasons. Species may not have been sufficiently introduced from local populations or their presence may have been obscured by other plants in the plot. Further, plots may have been selectively chosen to avoid exotic species where possible, as was the case in several project included in this dataset. In such sampling efforts, plots were chosen to represent the natural vegetation of a typical community type or geographic location. As such, patches dominated by native species were selected over nearby patches with exotic species presence, even if other characteristics of the community may have made the exotic-dominated patch more "representative" of the area. Even in plots with exotic species documented, the single description of the community does not provide sufficient detail about the trajectory of exotic populations (increasing, decreasing, cyclic, or stable). As such, the limited predictive ability of the environmental

characteristics may simply be reflective of the challenges in properly documenting exotic species population dynamics in a broad geographic region.

It is important to note that the exotic species involved in this broad analysis, while often similar to one another in origin and function, reflect unique life history traits and introduction patterns. Although general trends of exotic species presence are evident from these data, predictability of nuanced, individual species may remain elusive. The effort to address these specific responses among exotic species, analyzing common exotics for predictors of their presence, proved informative if unconvincing. The most significant correlates of unique exotic species presence, regardless of species, align with those of the entire dataset. In particular, metrics derived from the biotic community and soil fertility correlate with ESS most consistently, as is the case with the broader analysis. The nuanced correlates of individual species responses are most evident with *Celastrus orbiculatus*. This species' 5 environmental correlates, fewer than any other focal exotic species, are often of greater magnitude in significance. Perhaps most strikingly, its relation to cover of wetland species, one of the strongest correlates among all species, is opposite to that of the other focal invaders. Although *C. orbiculatus* tends to perform better in open woodlands and forest edges, it has exhibited significant shade tolerance capabilities (Ellsworth et al. 2004). These results suggest that this exotic species, while a threat to intact forests, should be considered more cautiously along habitat edges and in open stands and disturbed gaps. While such suggestions are typical of many exotic species, the results of this analysis indicate that this species may deserve more disproportionate emphasis in these areas than others.

The general patterns determined in this analysis suggest that exotic species do find success in novel environments due to multiple contributing factors associated with those

environments. Unfortunately, these local community characteristics do not provide significant predictive ability, due both to the lag times in exotic species success, alterations to disturbance regimes and local conditions, and unique biogeographic and life histories of both the exotic species and the communities to which they are introduced. The significance of the environmental variables in this study indicates that while many exotic species survive and reproduce due to their niche similarity to, and successful direct competition with, native species in local communities, numerous other exotic species successfully invade due to their unique exploitation of resources within the environment. It should be expected that, regardless of the life history and traits associated with any particular exotic species, the persistent role of propagule pressure in this region will enable further exotic species success in the future.

Conclusion

Exotic species success (ESS), the persistence of viable reproductive populations beyond initial colonization, is correlated with many environmental characteristics in plots across the southeastern Piedmont of the United States, including soil pH, available calcium, tree stem density and cover of wetland species. The unique predictive ability of any individual variable remains limited, reflecting the complex interactions that drive ESS in these communities and the range of biological attributes of the invaders. The best predictor of ESS is the dominant native species in a plot, given that its presence overlaps with and reflects multiple complementary environmental predictors. It is likely, however, with continued propagule pressure and human activity in these lands, that ESS will continue throughout this landscape and into previously unaffected communities due to the variety of conditions in which exotic species can survive and reproduce.

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Tables and Figures

Table 1. The 27 potential predictors of invasion used in this manuscript. A "/" in the "Variable" column indicates a distinct predictor variable with similar collection and analysis methods to the initially listed variable in the category.

Category	Variable	Units	Plots with this variable (1038 total)	Transformations	Data collection window	Resources used in assessment
Topography	Elevation	Meters	811		Time of sampling	GPS NAD 1983
	Slope	Degrees	752		Time of sampling	Klinometer
	Aspect	Degrees	658	Cos (aspect-45) (Beers et al 1966)	Time of sampling	Klinometer
Proximity	Distance to nearest stream	Decimal degrees	840	Decimal degrees to meters	Post-sampling calculation	EPA national hydrography dataset plus; ArcGIS
	Distance to nearest road	Decimal degrees	839	Decimal degrees to meters	Post-sampling calculation	State DOT primary/secondary highways; ArcGIS
Soil	Median soil depth	Meters	298		Time of sampling	117 cm soil probe
	Percent as organic matter	Percent	670	Log-transformed	Off-site analysis	Brookside laboratories
	Percent as sand/silt/clay	Percent	691		Off-site analysis	Brookside laboratories
	pH	n/a	753		Off-site analysis	Brookside laboratories
	Exchange capacity	meq/100 g	753		Off-site analysis	Brookside laboratories
	Base saturation	Percent	749		Off-site analysis	Brookside laboratories
	Bulk density	g/cm^3	749		Off-site analysis	Brookside laboratories
	Nitrogen	#'s N/acre	670		Off-site analysis	Brookside laboratories
	Soil sulfur	ppm	670	Log-transformed	Off-site analysis	Brookside laboratories
	Soil P/Ca/Mg/ K/Na	mg/kg	674	All: log-transformed	Off-site analysis	Brookside laboratories
Biotic community	Canopy basal area	$meters^2/$ ha	721	Log-transformed	Post-sampling calculation	Species records
	Density of tree stems	stems/ha	721	Log-transformed	Post-sampling calculation	Species records
	Native species of greatest cover		976		Post-sampling calculation	Species records
	Total native species richness (400 m^2)		1038		Post-sampling calculation	Species records
	Summed cover of obligate or facultative wetland species		1038	Log-transformed	Post-sampling calculation	Species records and national wetland plant list- U.S. Army Corps of Engineers
PCA	Principal component 1				Post-sampling calculation	

Table 2. The semi-log scale of cover estimates in CVS methodology (adapted from Peet et al. 1998).

Cover Code	Estimated Cover (%)	Cover Midpoint (%)	Cover Geometric Mean (%)
1	<0.1	0.05	0.03
2	0.1-1	0.5	0.10
3	1-2	1.5	1.41
4	2-5	3.5	3.16
5	5-10	7.5	7.07
6	10-25	17.5	15.81
7	25-50	37.5	35.36
8	50-75	62.5	61.24
9	75-95	85	84.41
10	95-100	97.5	91.47

Table 3. The most frequent exotic species in the dataset, each analyzed individually.

Exotic Species	Frequency in Dataset ("Invaded" Plots)	Number of "Uninvaded" Plots
Lonicera japonica	688	350
Ligustrum sinense	387	651
Microstegium vimineum	341	697
Elaeagnus umbellata	93	945
Celastrus orbiculatus	78	960
Rosa multiflora	70	968

Table 4. The 13 continuous variables with significant relationships with exotic species cover at all four establishment thresholds (1%, 2%, 5%, 10%), determined via standardized binomial regression and expressed by Wald test significance <0.05.

	1% Exotic Cover		10% Exotic Cover	
Predictor	Slope	Significance	Slope	Significance
Basal Area	0.670	8.95E-05	0.597	2.35E-02
Base Saturation	0.608	1.60E-11	0.439	2.22E-03
Bulk Density	-0.446	8.53E-04	-0.636	4.13E-02
Calcium	0.990	1.20E-17	0.737	4.02E-05
Elevation	-0.826	1.85E-08	-0.710	5.28E-03
Exchange Capacity	0.495	2.20E-09	0.350	3.22E-03
Magnesium	0.618	3.43E-10	0.375	1.54E-02
pH	0.763	3.34E-15	0.545	2.60E-04
Slope	-0.732	2.97E-08	-0.678	5.43E-03
Sodium	0.518	2.32E-08	0.336	2.11E-02
Stem Density	0.787	4.26E-13	0.760	2.74E-06
Sulfur	-0.397	2.03E-05	-0.377	1.63E-02
Wetland Species Cover	1.048	4.39E-37	1.145	5.75E-13

Table 5. The slope of the binomial regression for 22 standardized variables that are significantly related to invasion for at least one exotic species in the dataset. Significant slopes are shaded gray, as expressed by Wald test significance <0.05. The most frequent species tend to have more significant and greater magnitude correlations than those that are less frequent in the dataset, though the magnitude often varies with species.

Variable	*Lonicera japonica*	*Ligustrum sinense*	*Microstegium vimineum*	*Elaeagnus umbellata*	*Celastrus orbiculatus*	*Rosa multiflora*
Basal Area	0.70	1.21	1.39	0.44	0.91	0.69
Base Saturation	0.84	0.47	0.59	0.60	1.73	0.40
Bulk Density	-0.37	-0.56	-0.53	-0.28	-0.18	-1.27
Calcium	1.14	0.83	0.97	0.41	0.74	0.66
Distance to Road	-0.25	-0.34	-0.23	-0.05	-1.98	-0.26
Distance to Stream	-0.40	-0.67	-1.41	-0.07	-0.84	-2.18
Elevation	-1.09	-1.36	-1.05	-0.34	-2.16	-0.55
Exchange Capacity	0.77	0.42	0.46	0.00	-0.45	0.28
Magnesium	1.02	0.55	0.61	0.27	0.39	0.38
Native Richness	0.32	0.48	0.44	0.35	1.28	0.15
Nitrogen	-0.44	-0.33	-0.36	-0.40	-0.37	-0.11
Percent Clay	0.23	0.17	0.15	-0.34	-0.58	-0.01
Percent Organic	-0.43	-0.35	-0.39	-0.38	-0.60	-0.18
pH	0.98	0.60	0.73	0.68	0.93	0.50
Phosphorus	0.21	0.22	0.12	-0.19	0.09	0.03
Potassium	0.39	0.06	0.19	-0.06	-0.72	0.14
Slope	-0.49	-0.66	-0.95	-0.12	0.02	-0.73
Sodium	0.71	0.59	0.53	-0.01	0.05	0.42
Soil Depth	0.58	0.44	0.26	0.21	0.00	0.48
Stem Density	0.76	0.75	0.47	0.47	0.81	0.47
Sulfur	-0.53	-0.51	-0.41	-0.35	0.31	-0.14
Wetland Cover	0.91	1.17	1.10	0.31	-2.23	1.25

Significance: Wald test <0.05

Figure 1. CVS Plot Design, consisting of 10 modules, each 10x10 meters. Four modules are sampled intensively, collecting vegetation data at multiple spatial grains. Reproduced from Peet et al. (2012).

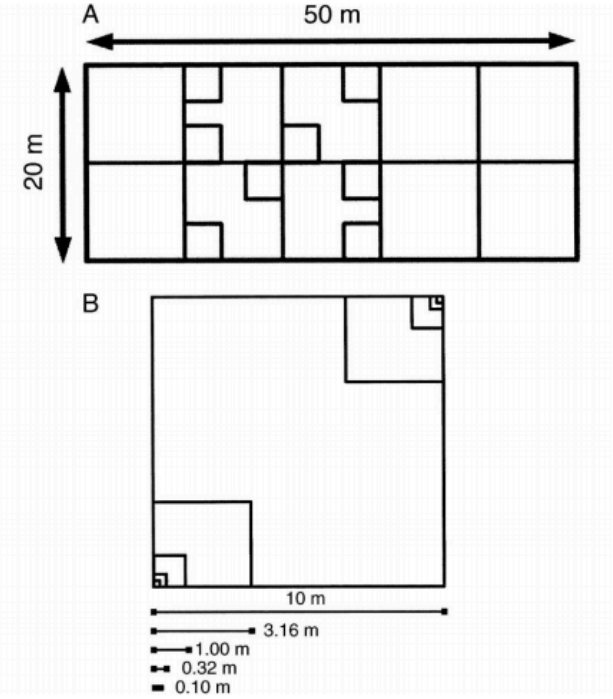


Figure 2. Map of the distribution of CVS plots used in this analysis.

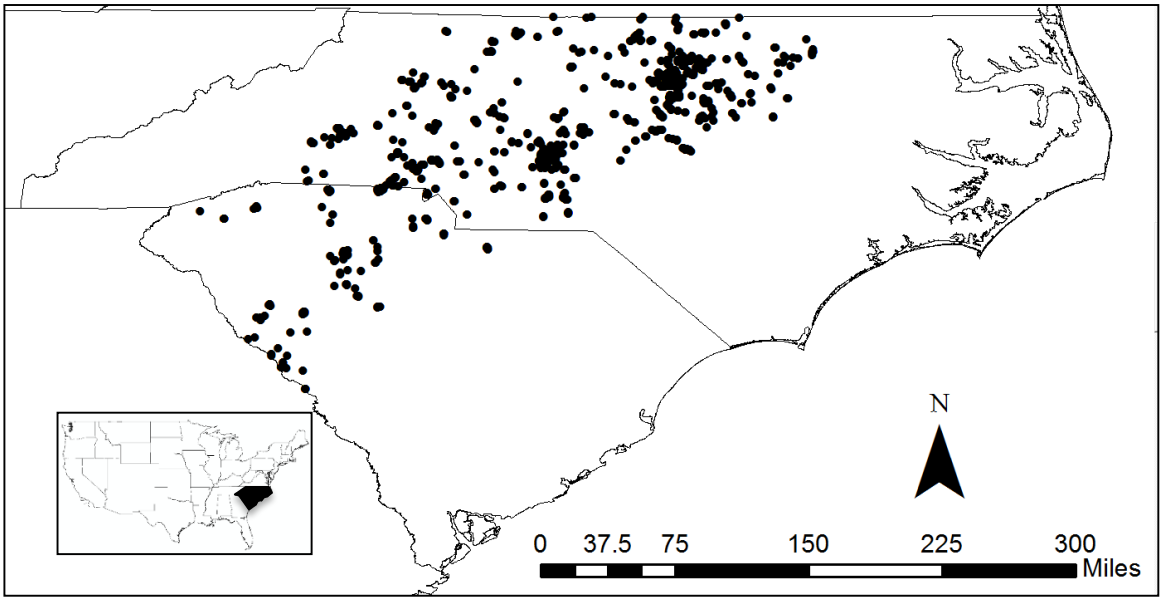


Figure 3. The percentage of plots in the dataset experiencing exotic species success, partitioned by the most dominant species within those plots. Plots dominated by typically xeric species, such as *Quercus spp.* (oaks) and *Carya spp.* (hickories), tend to have little exotic cover, as represented by the open data points. By contrast, plots dominated by mesic species, such as *Acer spp.* (maples) and *Liquidambar styraciflua* (sweetgum), typically have greater exotic cover, as represented by closed data points. This pattern holds across thresholds of exotic species cover and for the most frequent exotic species in the dataset.

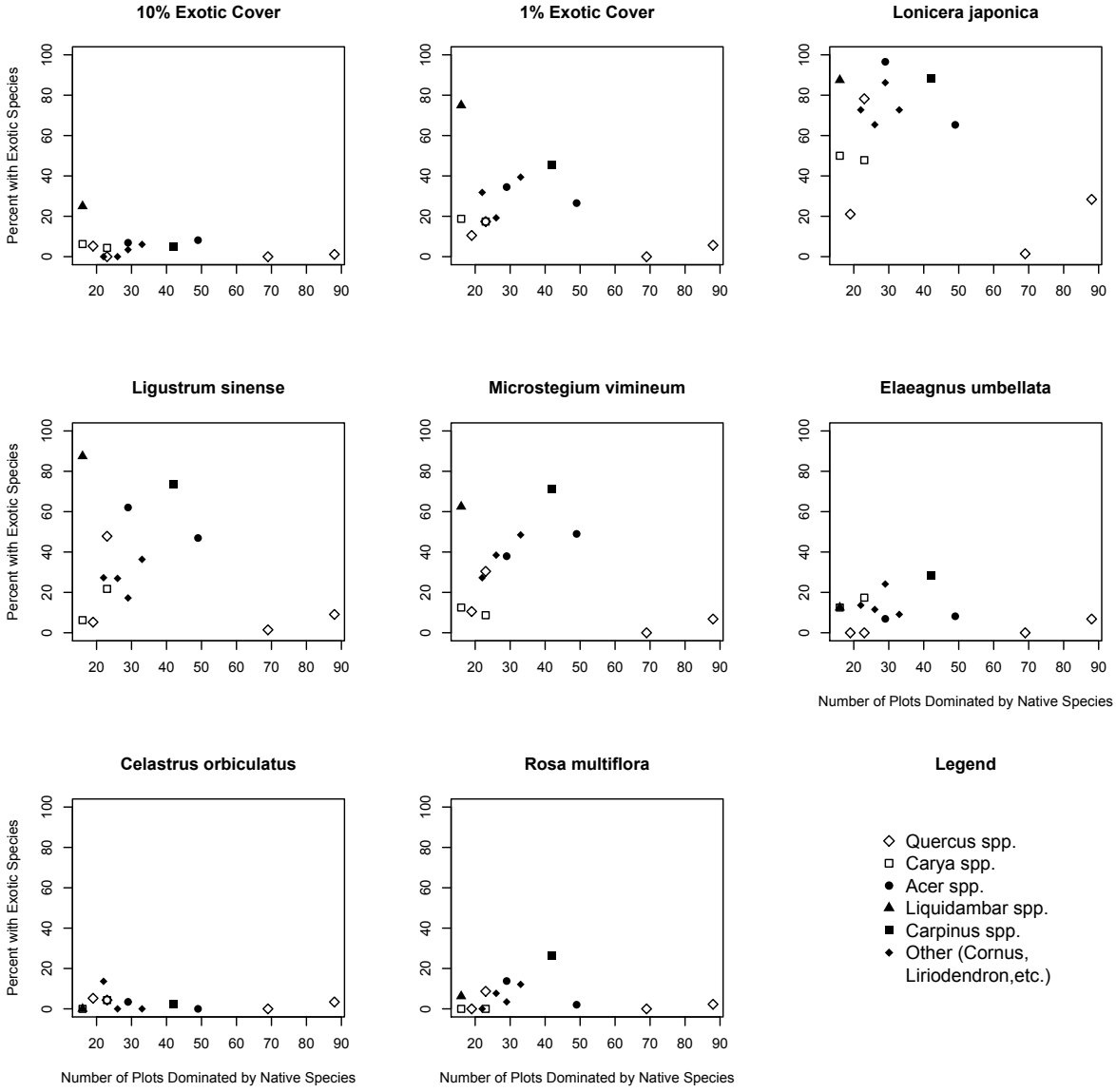


Figure 4. The relative importance of significant variables in predicting exotic species success, using the Lindeman, Meranda and Gold method of unweighted R^2 decomposition. The total response variance was partitioned to determine percent of exotic species cover patterns explained by using (A) only the four most significant continuous variables in predicting at least 5% exotic species cover in 640 plots and (B) ten most significant continuous variables in predicting at least 5% exotic species cover in 521 plots.

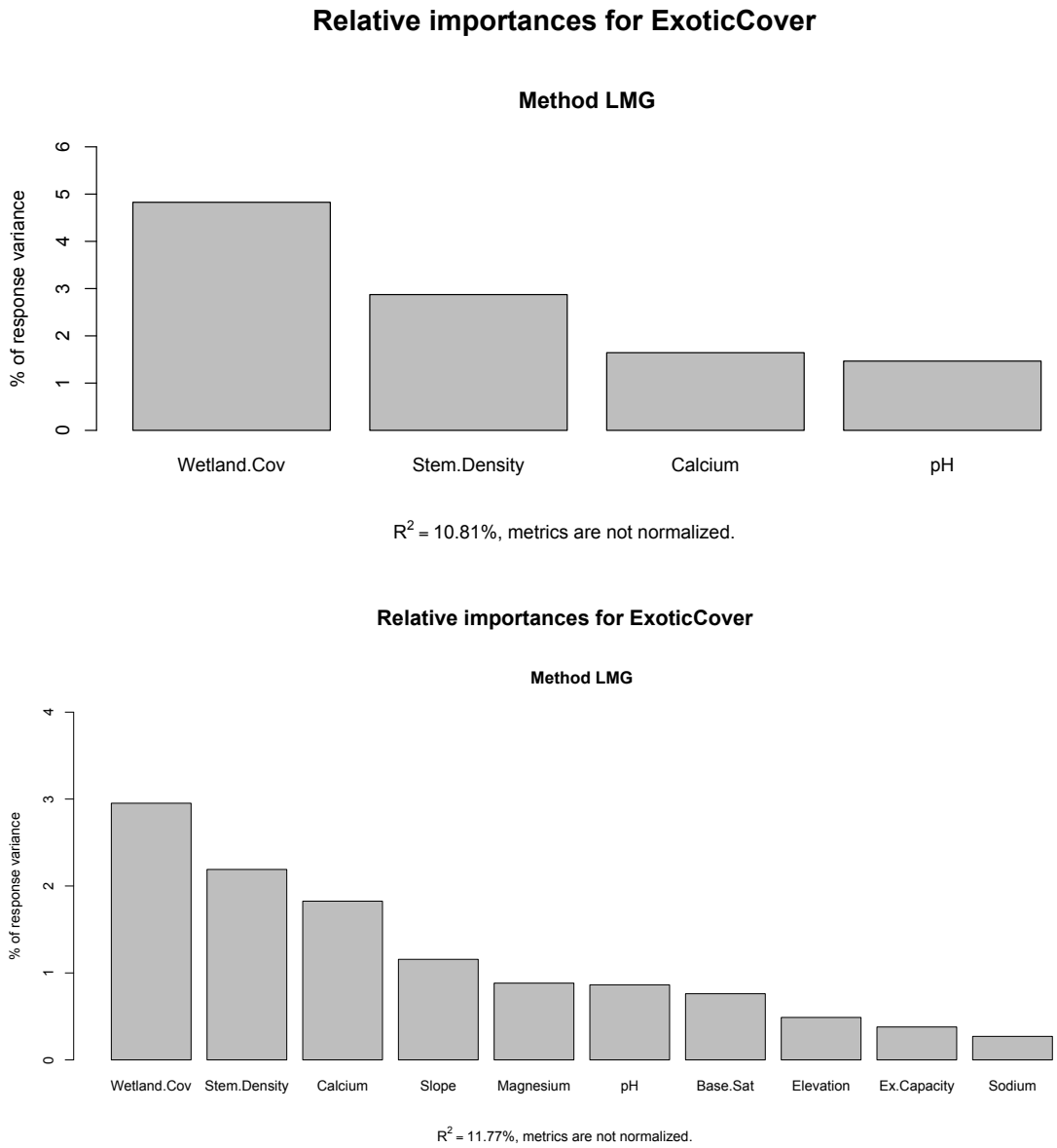


Figure 5. Classification and regression tree of standardized environmental variables in predicting exotic species success at 5% threshold in 1038 Piedmont plots. Each variable was standardized with the mean at 0, and all other values converted to the unit-free z score from the mean. Plots with <5% cover of exotic species, represented in the tree as a value of "0", were consistently similar in environmental conditions. This is indicated by the broad suites of conditions that express values approaching 0, meaning that the vast majority of plots in that group were uninvaded. However, few suites of environmental predictors can readily predict ESS, as evidenced by the few numbers approaching 1 in the analysis. Where ESS can be determined across the dataset, wetland species cover seems most effective in distinguishing sites with ESS.

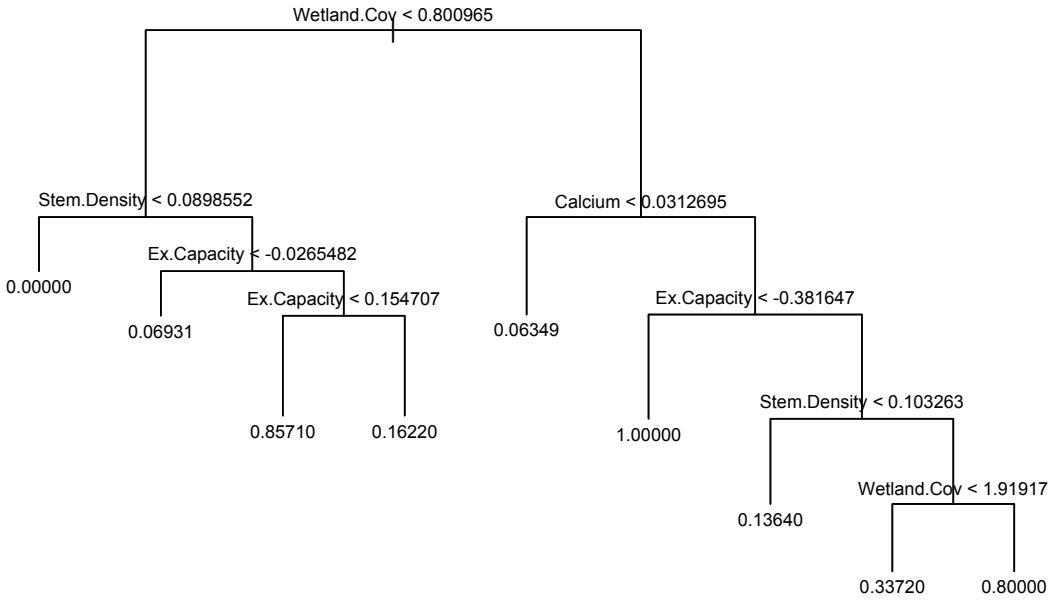
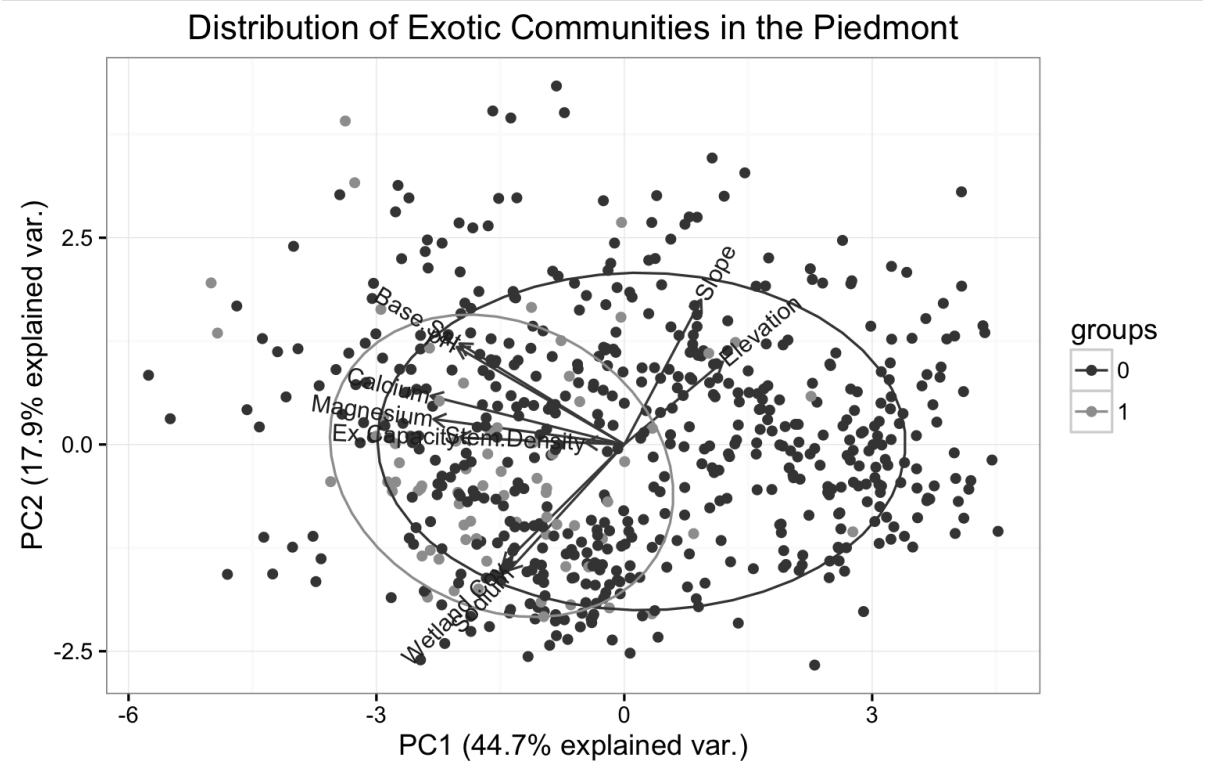


Figure 6. Principal components analysis of environmental variables distinguishing plots containing >5% exotic species (1, gray) and those without (0, black). No singular principal component readily predicts exotic species success, though several variables, namely wetland species cover and sodium content, are correlated with exotic species presence.



CHAPTER 4: SHRUB INVASIONS DIFFERENTIALLY AFFECT FOREST COMMUNITY RICHNESS AND STRUCTURE

Introduction

Invasive species pose a significant and immediate threat to conservation efforts around the globe (Bellard et al. 2016). The consequences of species invasions vary across systems and taxa. Traditionally, invasive species have been considered to be drivers of environmental change, successfully establishing in local communities and gradually out-competing neighbors (Merriam and Feil 2002). While invasive plants do not generally drive native species to extinction (Gurevitch and Padilla 2004, Bellard et al. 2016), they can locally outcompete native species to impact plant community composition and diversity across multiple scales (Hejda et al. 2009, Fukami et al. 2013). Prolonged invader dominance can reduce woody plant seedling regeneration (Duclos et al. 2014) and species diversity (Hart and Holmes 2013), eventually yielding severe canopy loss and above average tree mortality (Houston et al. 2010). Invasive plants can also disrupt below-ground interactions, thereby indirectly affecting native plant survival (Stinson et al. 2006) or leading to a changed mycorrhizal community favoring other native and exotic species (Bunn et al. 2015).

Research on invasive species often focuses on species richness and abundance (e.g. Simberloff and Von Holle 1999, Stohlgren et al. 2008). Impacts on richness in native communities are often quantified via the slope and intercept of species-area relationships, measuring species richness at multiple nested spatial grains. These analyses suggest that significant and quantifiable species losses often occur at small spatial grain due to

intraspecific competitive displacement (Brown and Peet 2003, Herben et al. 2004) yet are less detectable at larger scales (Powell et al. 2013). By contrast, broad analyses of plant systems often demonstrate no scale-dependent relationship between invasion and species richness (Stohlgren and Rejmánek 2014), suggesting that invasive plant impacts are context-dependent. Exclusively using species richness and abundance to quantify the impact of invasive species, however, may overlook impacts that are more nuanced or difficult to measure (Simberloff 2011). A reduction or increase of an important growth form or functional type within a plant community (e.g. saplings, vines, etc.), largely undetectable in studies of species richness, may drastically alter a community's trajectory and future composition. For example, a 90% reduction in hardwood saplings is relatively undetectable in terms of species richness, yet could have perilous long-term impacts on community structure, particularly with respect to biomass, canopy cover, and gap dynamics (see Duclos et al. 2014). Such results reframe the question of how invasive species impact communities and present a new approach that could be broadly applied to understand the impacts of invasive species.

Importantly, invader dominance may not be the direct driver of species loss and community change. Rather, the success of invasive species may reflect underlying or pre-existing changes in environmental conditions that encourage invasion (Wilson et al. 2013, Hagan et al. 2014). Consequently, it is imperative that researchers examining the impacts of species invasions consider the implications of underlying changes to environmental conditions in addition to potential direct competitive effects (Grarock et al. 2014).

Here I address three key questions:

1. Does shrub invasion reflect pre-existing differences in local environmental conditions?
2. How do metrics of species richness change with shrub invasion?
3. How do structural components of forests change with shrub invasion?

To address these questions, I paired highly invaded communities with communities experiencing limited invasion. I collected and analyzed abiotic soil and topographic characteristics of each plot in an effort to isolate the changes in biotic plot characteristics associated with the species invasions themselves, independent of potential changes in environmental correlates. Though several other studies have employed similar paired-plot methods to explore the impacts of invasive species (e.g. Powell et al. 2013), these studies have not fully determined that invaded and uninvaded sites are quantitatively similar in underlying environmental characteristics. Such studies have used proxies for abiotic measurements, including overstory tree composition and topographic position, prior to analyzing the differences between invaded and uninvaded communities. Measurements of soil nutrient and texture can assist in determining quantitative environmental differences associated with invasion and demonstrate that biotic differences are truly due to invasion and not reflective of environmental changes that also predict invasions.

Methods

Study Region

This study was conducted west-northwest of Charlotte in Gaston and Lincoln Counties, North Carolina (Figure 1). This region of the southeastern Piedmont is in an urban matrix and is predominantly secondary forest with a mix of pines and hardwoods. The

proximity of urban areas and a network of river systems provide many opportunities for introduction of exotic species. These large, forested patches with varying degrees of invasion provide an informative system in which to study the impacts of invasive plant dominance (see Matthews et al. 2011). All plots were sampled at one of 6 sites, each a large tract of Carolina piedmont forest on conservation lands managed or owned by the Catawba Lands Conservancy.

Data Collection

To examine the impacts of invasive species on plant communities, I identified two invasive shrubs to consider as focal invaders, *Ligustrum sinense* Lour. (Chinese privet) and *Elaeagnus umbellata* Thunb. (autumn olive). Each species was introduced from Asia for horticultural purposes and has since spread into natural areas throughout the southeastern United States. These species elicit a noticeable change in the physical structure of the forest, dominating the shaded understory with dense clumps of stems. I chose two similar focal invaders in similar communities, in an effort to develop more general insights regarding shrub invasions than typical single-species analyses.

I located forested plant communities that were dominated by one of these invasive shrubs, generally representing >50% cover within the community. I sampled these communities in 2014 using the methodology of the Carolina Vegetation Survey (Peet et al. 1998, 2012), which employs nested subplots at six spatial grains in 10 ares (1 are = 100 m^2) arranged in a 5x2 fashion (Figure 2). I identified all vascular plant species present at each grain using the nomenclature of Weakley's "Flora of the Mid-Atlantic and Southern States" (2015). I identified to species all stems extending at least 1.37 m from the ground, including shrub species and climbing vines. Diameter at breast height (DBH) of each identified stem

was binned into one of 11 size categories as per CVS protocol (0-1 cm, 1-2.5, 2.5-5, 5-10, 10-15, 15-20, 20-25, 25-30, 30-35, 35-40 and to nearest cm for larger stems). I recorded soil depth, slope, aspect, and elevation for each plot. Finally, I collected soil samples from the A horizon of each plot, collecting 250 g of soil at 5-20 cm below the soil surface from each intensively sampled module, and combining the samples for one plot-level representative sample.

For each invaded plot, I identified an uninvaded but otherwise similar forested location nearby, generally within 500 m of the originally plot. These communities were of similar slope, aspect and dominant canopy trees as the invaded communities, and local records indicate that they were of similar land-use history and disturbance regime as the invaded plots. However, these communities generally had a small but non-zero density of the focal invader, typically immature stems, thus suggesting the potential for future invasion. To control for changes in phenology and climate, I sampled these communities with the same protocol within one week of sampling the invaded plots. No communities sampled had a historical record of active management of invasives, and the invaded plots had only one significant invader to avoid possible interactions between co-invaders. This resulted in 52 plots: 13 plots each of stands dominated by *Ligustrum sinense* or *Elaeagnus umbellata*, and 13 matched comparison plots for each focal invader.

After completion of the field season, collected soils were oven dried at 50^0 C for 48 hours, sieved, weighed, and shipped to Brookside Laboratories Inc. for analysis. Nutrient analyses employed the Mehlich III method (Mehlich 1984), percent organic matter was determined by loss on ignition, and texture analysis employed the Bouyoucos hydrometer method (Patrick 1958). Total cation exchange capacity (meq/100g), pH, estimated nitrogen

release, easily extractable P, exchangeable cations (Ca, Mg, K, Na ppm), percent base saturation, soluble sulfur and bulk density values were determined for each sample.

I performed post-sampling calculations to quantify several topographic and biotic variables of potential value for predicting focal species invasions. I calculated each plot's straight-line distance to the nearest stream in ArcMap (9.3.1), using EPA National Hydrography Dataset Plus stream data (region 03N). I calculated each plot's straight-line distance to the nearest road centerline in the study region, using state DOT maps of primary and secondary roads in North Carolina. These maps depicted all public roads with at least one lane of traffic in each direction, thereby serving as a common corridor for vehicle movement. I tested each continuous predictor variable for normality of distribution, and transformed non-normal distributions as needed, such as aspect and soil nutrient content (see table 1 for transformations). I then standardized each variable individually, such that the mean measured value for each variable was converted to zero. All values for that variable were likewise converted to their corresponding z score for more uniform comparison of impacts between variables.

Data Analysis

To determine if any individual environmental variable was predictive of species invasion, I developed a generalized linear model of each standardized variable's relationship with invasion status for each focal invader, using a binomial distribution in the MASS package of R version 2.15.1 (R Core Team 2012). I calculated the slope of the regression line and the Wald test statistic to determine significance of each model (Legendre and Legendre 2012). To compare the paired plots according to environmental conditions, I performed a Principal Components Analysis of all soil and topographic characteristics of the sampled

plots. I calculated the pairwise distance in ordination space between every plot for each focal invader (13 plots each in comparison to the 25 other plots in the dataset), for a total of 325 pairwise distances for each focal invader. I compared the similarity values of paired invaded-uninvaded plots to the rest of its dataset's pairwise distances.

I analyzed changes in the species-area relationship by calculating the mean richness of all vascular species at each spatial grain within each plot, then calculating the mean richness value and standard deviation for each treatment group at each scale. I also calculated independent measures of exotic and native species richness in each plot for each treatment. Because the dominance and density of invasive species varied among plots, I also calculated the linear relationship between plot-level species richness and the number of focal invader stems. To examine if spatial grain influences this richness-invasion relationship, I calculated this linear regression both at the full plot level and for individual nested 100 m^2 subplots. In order to avoid spatial autocorrelation at the subplot level, I randomly selected one nested subplot from each plot. I then calculated the slope and correlation coefficients of the linear regression relationship between invasion and richness for subplots. I performed this random re-selection 99 times and determined the median slope, intercept, and significance value for each relationship.

To analyze the relationship between forest structure and invader density, I first grouped tree records into four general size classes; Canopy trees (>25 cm DBH), mid-story trees (10-25 cm DBH), understory trees (2.5-10 cm DBH), and saplings (0-2.5 cm DBH). Vine species and native shrub species were grouped in their own unique classes for analysis, regardless of size, resulting in six classes for analysis. I developed linear models of total density within each class as a function of focal invader density within each plot. To examine

if scale influenced structural impacts, I performed this linear regression both at the full plot level and for individual nested 100 m^2 subplots. In order to avoid spatial autocorrelation at the subplot level, I randomly selected one nested subplot from each plot. I then calculated the slope and correlation coefficients of the linear regression relationship between invasion and each structural group for subplots. I performed this random re-selection 99 times and determined the median slope, intercept, and significance value for each relationship.

Results

Ligustrum sinense dominance is not significantly correlated wth any important soil or environmental characteristic (Table 2). *Elaeagnus umbellata* dominance is significantly correlated with increased soil cation exchange capacity, phosphorus availability and calcium levels, as well as marginally significant relatave to increases in soil sand content and magnesium, boron and copper levels. The pairwise distances of principal components analysis (Table 3) demonstrate that paired invaded and uninvaded communities are typically more similar to each other via abiotic and topographic measures than the vast majority of other plots in the dataset. The median paired invaded-uninvaded *L. sinense* plot was more similar than 74% of all other *L. sinense* pairings and the median paired invaded-ininvaded *E. umbellata* plot was more similar than 63% of all other *E. umbellata* pairings. Although some pairs in each dataset reflected substantial differences in abiotic conditions relative to other communities, these differences were not consistent with any significant change in levels of invasion or other differences in community metrics in this analysis (Table 3).

The mean species-area relationship in paired and unpaired communities (Figure 3) is not significantly different across most scales or measures. Mean total species richness is not significantly different for any invasion group at any scale. Although native species richness is

visually lower in invaded *L. sinense* plots than in paired control plots at the two smallest spatial grains, this value is not significantly different at any scale. Exotic species richness is significantly higher in invaded *E. umbellata* plots than their relative controls at all scales up to 100 m^2, but is not significantly different at larger scales for either focal invader. When the focal invader is excluded from the dataset, the exotic species-area relationship is non-significant between invaded and uninvaded sites for either focal species, but is significantly higher in both control and invaded plots associated with *L. sinense* than in plots associated with *E. umbellata* (Figure 4).

Ligustrum sinense stem density correlates with a marginally significant decline in total plot-level species richness and a significant decline in native species richness at the plot level, the only statistically significant relationship of any variant of richness metrics at the plot level (Table 4). The significance of these relationships is reinforced by a drastic decline in species richness in the plot with the highest *L. sinense* density. The slopes of these relationships remain similar if this data point is excluded, however, indicating that this significant species decline with high *L. sinense* density simply magnifies a trend that is consistent at lower levels of invasion. Both total species richness and native species richness are significantly and negatively correlated with *L. sinense* stem density at the 100 m^2 subplot level, suggesting that invasion impacts may be more prevalent at small spatial grain. *E. umbellata* stem density is not significantly correlated with any measure of species richness at either scale of investigation.

Forest community structure responds to changes in *L. sinense* density in different fashions at the plot and subplot levels. *Ligustrum sinense* stem density is correlated with significant plot-level decreases in sapling and lower-story trees (Figure 5), marginally

significant decreases in mid-story trees, shows no relationship in canopy trees, and shows significant increase with shrub and vine frequency. At the subplot level, however, *L. sinense* stem density is correlated with marginally significant increases in canopy trees and significant increases in shrub and vine frequencies. There is no statistical relationship between *L. sinense* stem density and subplot measures of sapling, understory trees, and mid-story trees (Table 4). *E. umbellata* stem density correlates with a significant decrease in plot-level sapling density, but is not significantly related to any other structural group. At smaller spatial grain, however, *E. umbellata* stem density is correlated with canopy trees and mid-story trees. There is no statistical relationship between *E. umbellata* stem density and subplot measures of saplings, understory trees, native shrubs, or vines.

Discussion

Invaded and uninvaded communties are not significantly different from each other by most measured abiotic or topographic metric. Increases in soil exchange capacity, phosphorus and calcium with *Elaeagnus umbellata* establishment reflect physiological traits of this focal invader. Because *E. umbellata* is capable of symbiotic nitrogen fixation, phosphorus often becomes a limiting resource for its survival (Vance 2001), as can calcium (Banath et al. 1966). *E. umbellata* invasion in these plots, therefore, may be reflective of historical differences in these characteristics that limit invasion in control plots, and *E. umbellata* can be predicted by properly sampling these soil characteristics (Grarock et al. 2014).

It should be noted that the plots in this dataset do not reflect a random sampling of vegetation communities throughout the study region. Rather, these paired plots were selectively chosen due to their potential for exotic shrub invasion, either via visual evidence

of invasion or similar environmental conditions to a nearby invaded plot. In this way, I sampled a narrow range of environmental conditions for correlates of exotic species success, reducing the potential for such correlates to emerge. When comparing plots experiencing invasion to a broader landscape of communities, many biotic and abiotic correlates might emerge that were not detected in this analysis (Chapter 3).

Despite the analyzed dataset representing a small subset of similar communities across a relatively small landscape, most of the invaded communities were more similar in environmental conditions to their paired uninvaded counterparts than to other invaded communities. These results suggest that *Ligustrum sinense*, in particular, is not generally exploiting environmental differences to opportunistically invade select pockets of a landscape due to disturbance or resource availability gradients. These findings allow us to compare invaded and uninvaded communities with greater confidence that detected differences in biotic measures are due to, and not simply co-occuring with, species invasions. Although *E. umbellata* invasion may be predicted by underlying differences in phosphorus, calcium and exchange capacity, the limited responses to invasion in associated biotic metrics relative to *L. sinense* invasion suggests that *E. umbellata* may be less of a conservation and management concern. Proximity metrics such as distance to the nearest stream or nearest road were generally unpredictive of successful invasion for either species, suggesting that currently uninvaded communities are not immune to species invasions due to geographic or topographic factors; indeed, these communities are likely to experience future invasion with continued exotic encroachment and propagule pressure of nearby seed sources. This prediction is evidenced by the numerous immature stems of focal invaders found in the uninvaded plots, indicating the potential for continued establishment in those plots. Although

invader success is often strongly correlated with land-use history (Lundgren et al. 2004) or altered disturbance regimes (Nagler et al. 2005), the similarity of land-use history in these paired plots precludes this historical aspect from predicting establishment.

The limited differences in species-area relationships with invasion corroborate previous conclusions that communities are not responding to invasion unilaterally, instead they appear to be reflecting a generally small and nuanced response to species invasion (Vila et al. 2011, Simberloff et al. 2013, Davis et al. 2015). Mean total species richness is not significantly different for any invasion group at any scale. Native species richness is marginally significantly lower in invaded *L. sinense* sites than in its control at the two smallest spatial grains, but is not significantly different at any other scale. These results indicate that species invasions are not generally reflective of complete extirpation at a community scale, though exotic dominance may lead to small-scale out-competing of native species. These findings corroborate previous and similar paired-plot empirical studies (Powell et al. 2013). Beyond changes in species richness metrics, invaded areas may experience context-dependent responses in regional species turnover (Lososova et al. 2016), or exotic species may simply augment the regional flora in a non-significant manner (Thomas and Palmer 2015) resulting in interactions that evade detection by simple species richness metrics.

Exotic species richness is significantly higher in both sets of invaded plots than their relative controls at all scales up to 100 m^2, but is not significantly different at larger scales for either focal invader. These data include the focal invader, indicating that heavily-invaded communities exhibit a greater density of the focal invader at many smaller scales, as expected. After removing the focal invader from the exotic richness analysis, however,

exotic species richness in invaded communities remains significantly higher than controls at most scales. These data suggest that exotic species are often successful concurrently. Although abiotic conditions do not seem to drive these patterns of establishment, the process of invasional meltdown (Simberloff and von Holle 1999) may explain the patterns emerging in these communities. In particular, successful exotic shrub establishment and dominance may facilitate exotic vines or shade-tolerant herbs, due to the increased amount of anchor points and shade, respectively, provided by a dense shrub layer. It is not likely that the increased presence of co-occurring exotic species in invaded plots is due to an increase in propagule pressure, as invaded plots did not differ from control plots for either species in proximity metrics, such as distance to roads or rivers.

The declines in total species richness with *L. sinense* stem density at multiple spatial grains suggest that varying density of invasive populations may yield differential effects on communities (Jackson et al. 2014). The lower slopes in both total and native richness values at smaller spatial grain indicates that small-scale impacts of invasive species may be more significant than at larger scales, consistent with previous findings (Powell et al. 2013). Alternatively, large-scale responses to invasion occur over larger time scales.

These data indicate that *E. umbellata* invasion appears to have a smaller impact on the biotic community than *L. sinense* invasion. Given the structure of both *E. umbellata* and *L. sinense*, where *E. umbellata* is a spreading shrub with flexible stems and *L. sinense* is generally more erect, it is logical that *L. sinense* stems can reach a much greater density than *E. umbellata* in communities of similar size (nearly 3x as dense), thereby exerting greater impacts on communities. Despite its decreased stem density in highly invaded plots, *E. umbellata* may, nonetheless, foster detectable changes in biotic communities that are beyond

the scope of this work. For example, the nitrogen fixation capabilities of *E. umbellata* symbionts, coupled with lag effects in biotic responses to environmental change, may yield future responses in richness and structural metrics.

Both *L. sinense* and *E. umbellata* stem density correlate with significant decreases in plot-level sapling densities, indicating that a dense shrub layer may be effective in directly out-competing light-dependent tree species. Alternatively, exotic shrub dominance may yield reduce tree regeneration due to less apparent indirect interactions, particularly via harboring more seed predators (Meiners 2007, Orrock et al. 2008). Regardless of the mechanism of reduction, however, this loss of tree regeneration may prove a concerning concern with respect to forest regeneration.

Because *E. umbellata* does not form such impenetrable layers as *L. sinense*, it is unsurprising that it has no detectable impacts on plot-level tree stem densities for medium-sized and larger canopy trees. Likely, interspecific competition from *E. umbellata* is replacing intraspecific competition among saplings, such that self-thinning pressures are diminished among these tree species. Those small trees that do penetrate the shrub layer are likely unaffected by the dense shrub layer below, growing to canopy trees at a similar rate as in uninvaded communities. By contrast, *L. sinense* dominance yields significant decreases in understory trees and marginally significant decreases in mid-story trees, indicating that the more erect and dense stems of *L. sinense* are more effective in outcompeting tree species than *E. umbellata*. Although there is no statistical plot-level relationship between *L. sinense* stems and canopy trees, this may be due to the long-lived nature of canopy trees and the relatively short time span of *L. sinense* invasion. Because these impacts are manifested with mid-story trees and are not reflective of drastic changes in abiotic conditions, it is possible that canopy

response to *L. sinense* invasion will occur over the next several decades (Hartman and McCarthy 2007). Alternatively, like *E. umbellata* invasion, *L. sinense* invasion may simply replace understory tree thinning and reach a threshold of interspecific competition with tree species, beyond which those trees that survive will remain in similar frequencies in the canopy.

The relationship of focal invader density and subplot-level structural metrics differs for several structural groups. The marginally significant, though quite small, relationship between subplot-level canopy tree density and stem density for each focal invader suggests that environmental heterogeneity, particularly gap dynamics and small-scale disturbances, may enable exotic shrub establishment (Nagler et al. 2005). This may also be a suitable explanation for the significant relationship between mid-story tree presence and *E. umbellata* density. The insignificant relationship between *L. sinense* stem density and subplot saplings, understory trees, and mid-story trees, demonstrates a stark contrast from plot-level structural dynamics. This loss of significance with decreasing scale also counters the pattern seen for species richness metrics, where small-scale changes were generally more significant than larger-scale patterns. This loss of significance may be reflective of the small number of tree stems in each group at this smaller scale, such that losses may not be captured at a fine spatial grain and can only be effectively quantified on larger scales. This interaction likely also explains the loss of significance in the relationship between *E. umbellata* density and subplot-level sapling density.

Ligustrum sinense stem density correlates with significant increases in native shrubs at both examined scales. Although seemingly counterintuitive, native shrubs are very fast-growing and may be more capable than tree species of persisting with changes in light and

resource availability. In addition, the increase in shade in *Ligustrum*-dominated communities may provide more favorable conditions for shrub growth regardless of species. Finally, *L. sinense* stem density significantly predicts increases in vine frequencies, suggesting facilitation due to the increased amount of anchor points provided by a dense shrub layer.

Conclusion

Density of *Ligustrum sinense* and *Elaeagnus umbellata*, two exotic shrubs currently invading the southeastern United States, correlates with distinct changes within the communities they invade. Although *L. sinense* invasion is not accurately predicted by most environmental characteristics of interest, it does correlate with losses in species richness at multiple spatial scales, as well as losses in saplings and small trees at large scales and increases in vines and shrubs at multiple scales. The collective community response to this invasion suggests a dire prognosis for the future of invaded communities. By contrast, *E. umbellata* invasion can be predicted by several soil nutrients, and its impacts seem limited to some loss of saplings only at large scales. Although quite similar in form, origin, and invasion level, these two shrub invasions demonstrate that community responses to invasion vary dramatically.

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Tables and Figures

Table 1. The 21 potential predictors of invasion used in this manuscript. A "/" in the "Variable" column indicates a distinct predictor variable with similar collection and analysis methods to the initially listed variable in the category.

Category	Variable	Units	Transformations	Data collection window	Resources used in assessment
Topography	Elevation	Meters		Time of sampling	GPS NAD 1983
	Slope	Degrees		Time of sampling	Klinometer
	Aspect	Degrees	Cos (aspect-45) (Beers et al 1966)	Time of sampling	Klinometer
Proximity	Distance to nearest stream	Decimal degrees	Decimal degrees to meters	Post-sampling calculation	EPA national hydrography dataset plus; ArcGIS
	Distance to nearest road	Decimal degrees	Decimal degrees to meters	Post-sampling calculation	State DOT primary/secondary highways; ArcGIS
Soil	Median soil depth	Meters		Time of sampling	117 cm soil probe
	Percent as organic matter	Percentage	Log-transformed	Off-site analysis	Brookside laboratories
	Percent as sand/silt/clay	Percentage		Off-site analysis	Brookside laboratories
	pH	n/a		Off-site analysis	Brookside laboratories
	Exchange capacity	meq/100 g		Off-site analysis	Brookside laboratories
	Base saturation	Percentage		Off-site analysis	Brookside laboratories
	Bulk density	g/cm^3		Off-site analysis	Brookside laboratories
	Nitrogen	#'s N/acre		Off-site analysis	Brookside laboratories
	Soil sulfur	ppm	Log-transformed	Off-site analysis	Brookside laboratories
	Soil P/Ca/Mg/ K/Na	mg/kg	All: log-transformed	Off-site analysis	Brookside laboratories

Table 2. The slope of the binomial regression between focal invader dominance and 21 standardized environmental variables for the 26 plots associated with each focal invader. Significant slopes are shaded gray, as expressed by Wald test significance <0.05.

	L. sinense Invasion		*E. umbellata* Invasion	
Standardized Variable	Slope	Pr(>|z|)	Slope	Pr(>|z|)
Exchange Capacity	0.11	0.775	1.09	0.031
pH	0.60	0.255	0.49	0.201
Nitrogen Release	-0.27	0.452	-0.36	0.567
Sulfur	-0.23	0.513	0.48	0.237
Phosphorus	0.02	0.965	0.93	0.030
Calcium	0.13	0.805	1.26	0.060
Magnesium	0.75	0.245	1.15	0.070
Potassium	0.27	0.593	0.66	0.174
Sodium	0.12	0.797	0.23	0.527
Bulk Density	-0.31	0.600	0.48	0.284
Percent Organic Content	-0.18	0.652	-0.46	0.525
Percent Clay	-1.45	0.179	-0.73	0.314
Percent Silt	-0.13	0.723	-0.79	0.167
Percent Sand	0.35	0.359	1.03	0.075
Elevation	-0.66	0.213	-0.13	0.751
Aspect	-0.04	0.919	-0.40	0.294
Slope	0.19	0.709	0.17	0.706
Distance to Water	-0.50	0.530	-0.31	0.444
Distance to Road	0.98	0.114	-0.16	0.641
Soil Depth	0.60	0.158	1.19	0.357

Significance: p<0.05; p<0.10

Table 3. The median distance in PCA ordination space of environmental conditions for plots associated with each focal invasive shrub species. For both focal species, the paired plots were more similar to one another in environmental conditions than randomly selected plots from the dataset, indicating a similarity of environmental conditions, relative to the species distribution throughout the region.

	Ligustrum sinense	*Elaeagnus umbellata*
All plots	8.05	7.72
Paired plots	6.03	6.87
Median percentile of paired plots	74.46	63.69

Table 4. Slope, intercept and significance of structural changes with changes in focal stem density at both the plot (1000 m^2) and sub-plot (100 m^2) level.

	Plot-Level *L. sinense* Invasion			Random Subplot *L. sinense* Invasion		
Metric	Slope	Intercept	P-Value	Median Slope	Median Intercept	Median P-Value
Total Richness	-0.0035	61.1	0.07	-0.036	34.5	0.006
Native Richness	-0.004	56.3	0.02	-0.035	31.2	0.004
Exotic Richness	0.0005	4.1	0.17	-0.0007	3.0	0.5
Saplings	-0.054	182	0.025	0.002	25	0.43
Small Trees	-0.018	64.1	0.0008	0.003	9.3	0.44
Mid-Story Trees	-0.0046	33	0.074	0.007	4.6	0.11
Canopy Trees	-0.00093	17.4	0.6	0.005	2.3	0.06
Native Shrubs	0.03	32.9	0.006	0.03	5.3	0.02
Vines	0.152	149	0.00008	0.19	24.2	0.00003
	Plot-Level *E. umbellata* Invasion			Random Subplot *E. umbellata* Invasion		
Metric	Slope	Intercept	P-Value	Median Slope	Median Intercept	Median P-Value
Total Richness	-0.00098	61.7	0.86	-0.012	34.5	0.58
Native Richness	-0.00082	56.6	0.87	-0.016	31.8	0.52
Exotic Richness	0.00046	4.0	0.58	0.006	2.4	0.15
Saplings	-0.24	304	0.041	0.05	41.6	0.59
Small Trees	-0.04	105	0.26	0.06	13.3	0.13
Mid-Story Trees	0.0023	32.3	0.77	0.027	4.4	0.02
Canopy Trees	-0.0004	17.7	0.95	0.021	1.98	0.055
Native Shrubs	-0.003	7.7	0.81	0.0007	0.38	0.61
Vines	0.03	65.2	0.68	0.06	7.1	0.23

Significance: $p<0.05$; $p<0.10$

Figure 1. Geographic distribution of 52 sampled communities in a paired-plot empirical design, WNW of Charlotte, NC. 13 plots each were invaded by either *Ligustrum sinense* or *Elaeagnus umbellata*, each with a paired, uninvaded plot nearby.

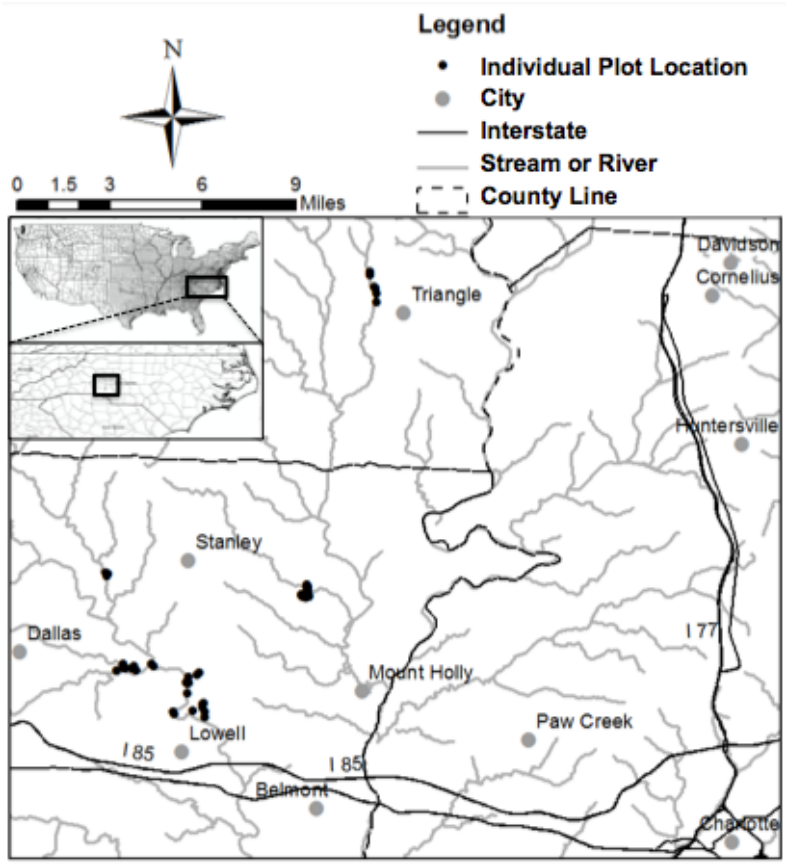


Figure 2. Plot design for CVS methodology, with 8 corners sampled intensively at 0.01, 0.1, 1, and 10 m^2 spatial grains. (Reproduced from Peet et al. 2012)

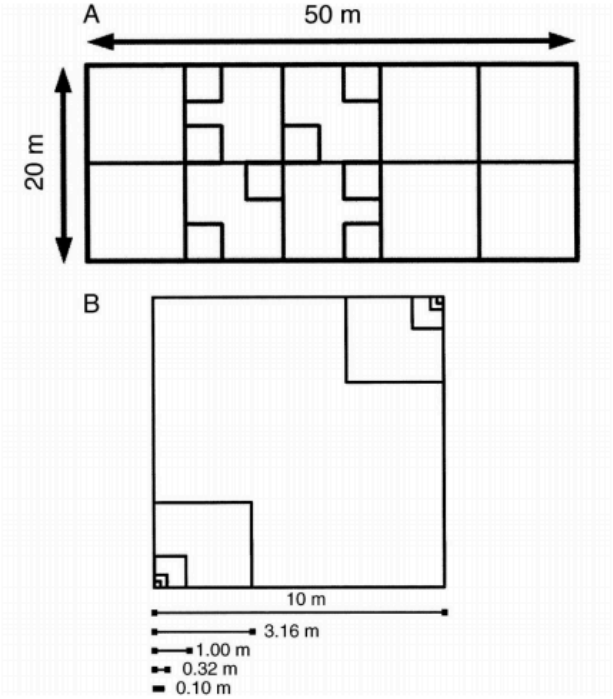


Figure 3. Mean species-area relationship for three distinct richness metrics. (A) Mean total species richness is not significantly different for any invasion group at any scale. (B) Native species richness is visually lower in invaded *L. sinense* sites than its control at the two smallest spatial grains, but is not significantly different at any scale. (C) Exotic species richness is significantly higher in invaded *E. umbellata* plots than their relative controls at all scales up to 100 m^2, but is not significantly above that scale for either focal invader.

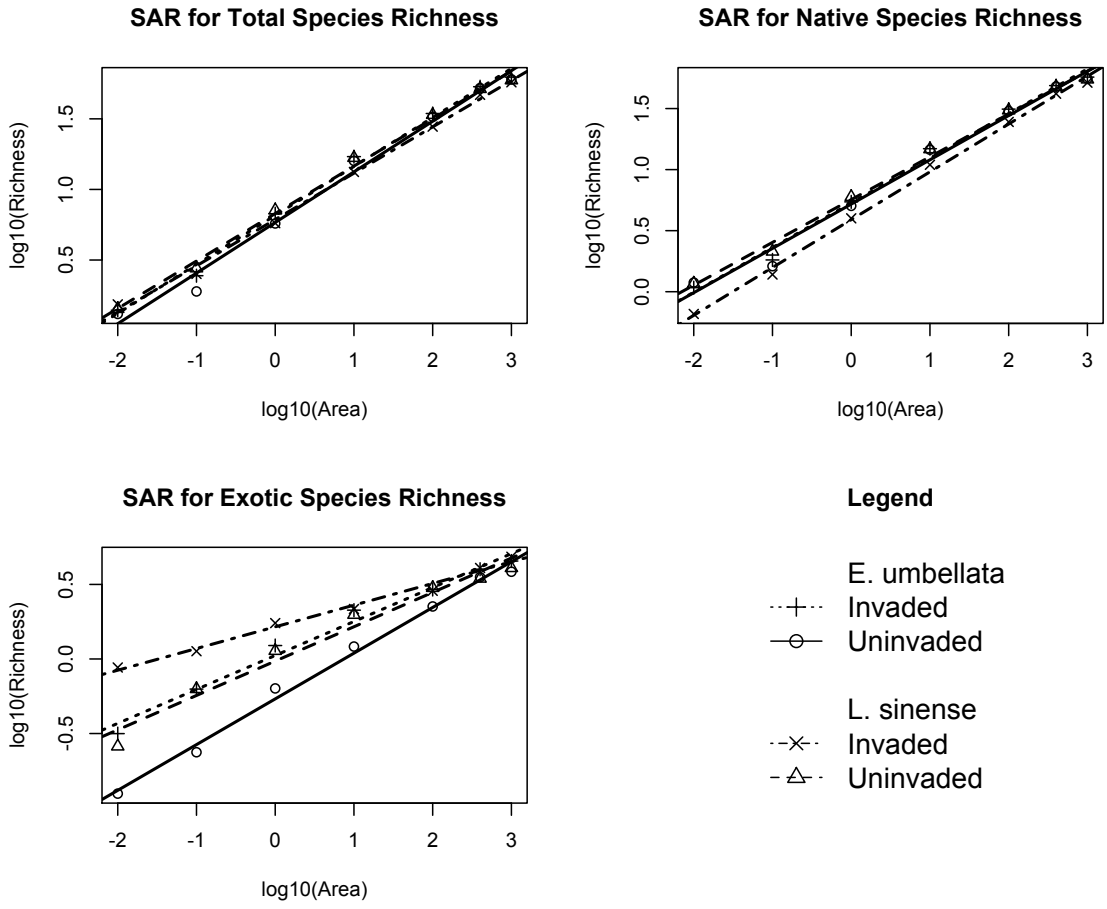


Figure 4. Species-area relationship for exotic species in invaded and uninvaded plots. There is no significant difference between invasion types for either focal invader, but there are significant differences among plots associated with focal invaders. There is a nonsignificant increase in exotic species richness in invaded plots compared to the control across all scales, indicating that species invasion may be facilitating limited amounts of co-invasion.

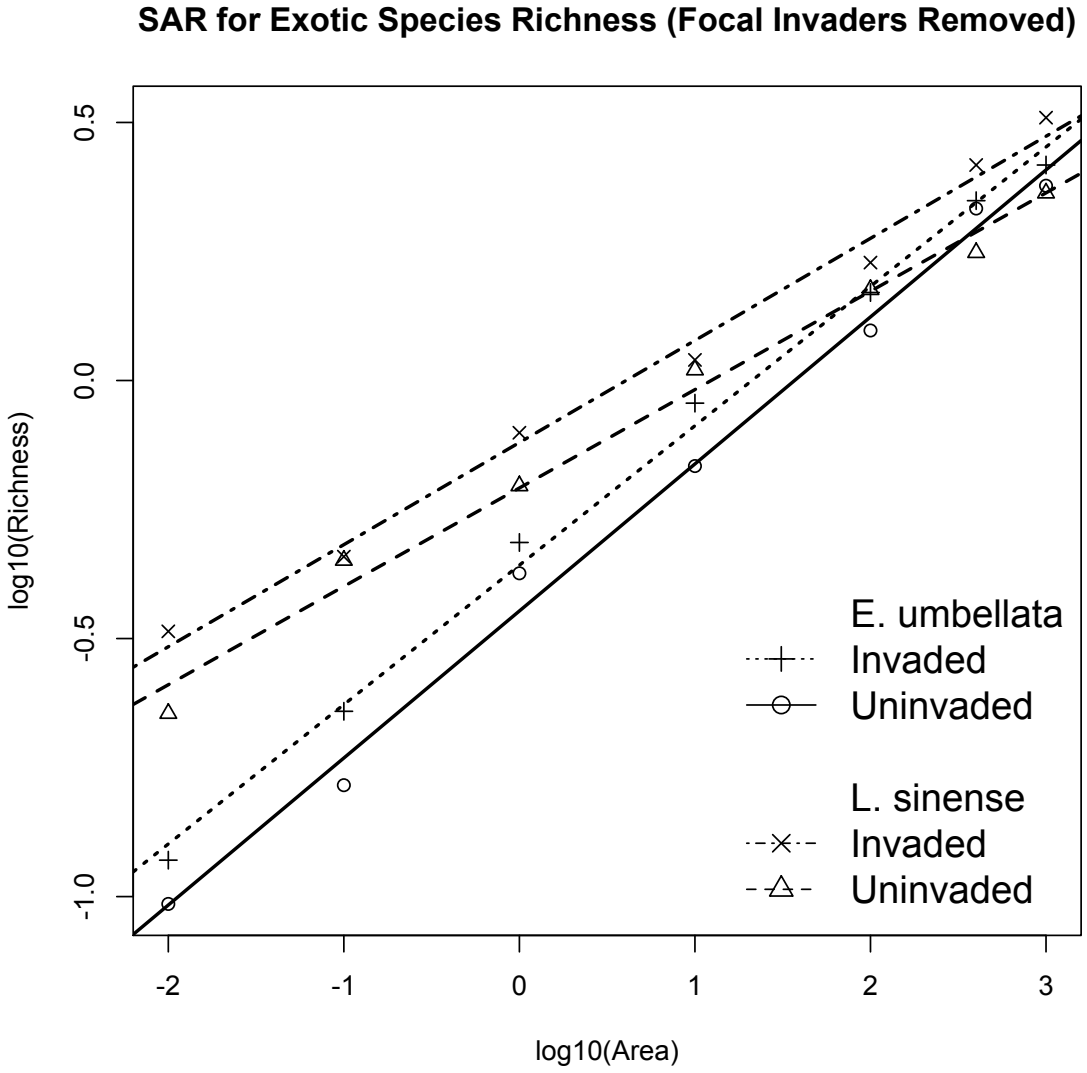
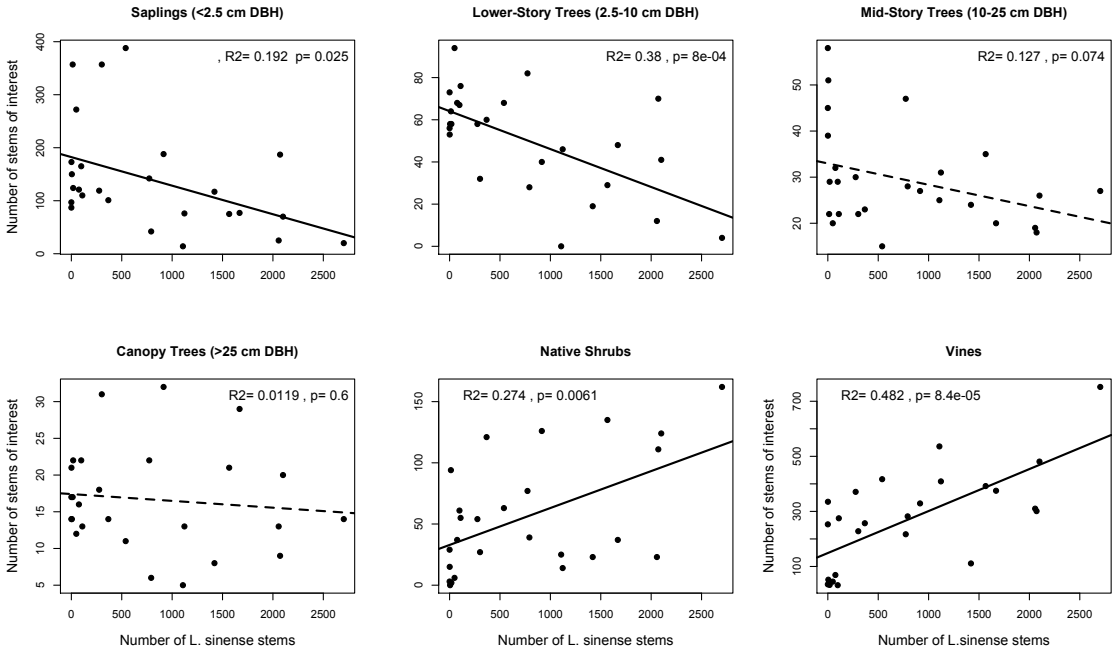
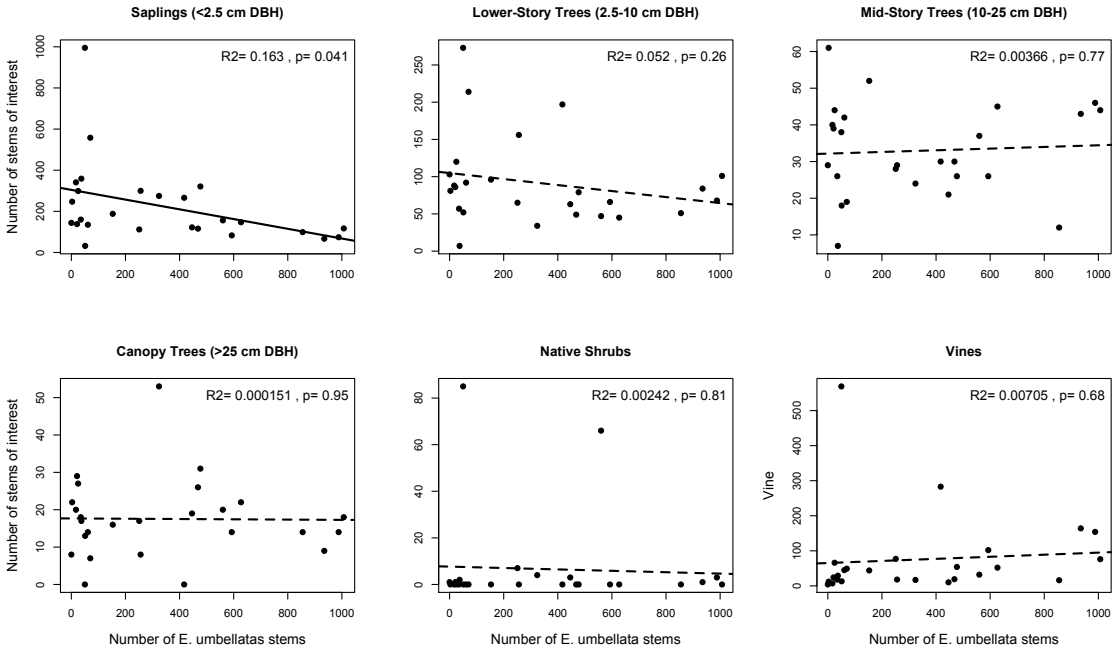


Figure 5. The relationship of plot-level structural groups and the continuous predictor of number of focal invader stems at breast height. Significant relationships are denoted by a solid line.

A: *Ligustrum sinense* stem density



B: *Elaeagnus umbellata* stem density



CHAPTER 5: EXPERIMENTAL REMOVAL OF DOMINANT INVASIVE SHRUBS CAUSES ABIOTIC RESPONSES IN FORESTED COMMUNITIES

Introduction

Invasive species pose a significant and immediate threat to conservation efforts around the globe (Bellard et al. 2016). Traditionally, invasive species have been considered as drivers of environmental change, successfully out-competing neighbors (Merriam and Feil 2002) or disrupting belowground interactions (Stinson et al. 2006). There remains need and demand, however, for analyses that examine changes in environmental conditions associated with species invasions.

Although some studies suggest that only limited environmental correlations exist with invader dominance (Wilson et al. 2013), species-specific patterns may emerge with sufficient sampling (Hagan et al. 2014). Many invasive plant species are capable of modifying ecosystem processes of natural systems to some magnitude (Gordon 1998), although such impacts vary with both the species invading (Vila et al. 2011) and the density of invading populations (Jackson et al. 2014). In particular, environmental transformers, such as the nitrogen-fixing *Elaeagnus umbellata*, can affect soil nutrient characteristics (Goldstein et al. 2009). Similar shrubby dominants, such as *Ligustrum sinense,* may not cause any significant changes in soil conditions (Devine and Fei 2011). It is important, therefore, to consider environmental changes with invasion across multiple sites and species to detect general patterns associated with species invasions.

Here I address three key questions regarding species invasions:

1. How do invaded and uninvaded communities differ in temperature, light availability, and soil moisture?
2. How does experimental removal of invasive shrubs affect measures of temperature, light availability, and soil moisture?
3. How does experimental removal of invasive shrubs affect measures of soil nutrient composition and texture?

To address these questions, I examined changes in communities with invasion of one of two focal invasive shrubs, *Elaeagnus umbellata* or *Ligustrum sinense*. I sampled vegetation plots in highly invaded communities nearby communities experiencing limited invasion, then collected and analyzed abiotic soil and environmental characteristics of each plot in an effort to assess abiotic changes associated with invasions. I then experimentally removed the focal invader from invaded plots to quantify the abiotic changes associated with their removal.

Methods

Study Region

This study was conducted west-northwest of Charlotte in Gaston and Lincoln Counties, North Carolina (Figure 1). This region of the southeastern Piedmont is in an urban matrix and is predominantly secondary forest with a mix of pines and hardwoods. These large, forested patches with varying degrees of invasion provide an informative system in which to study the impacts of invasive plant dominance (see Matthews et al. 2011). All plots were located at one of 5 sites, each a large tract of Carolina piedmont forest on conservation lands managed or owned by the Catawba Lands Conservancy.

Data Collection

This study employed sites and data used in a previous study (see Chapter 4), in which I examined the impacts associated with one of two focal shrub invaders, *Ligustrum sinense* Lour. (Chinese privet) or *Elaeagnus umbellata* Thunb. (autumn olive). These species elicit a noticeable change in the physical structure of the forest, dominating the shaded understory with dense clumps of stems. In the summer of 2014, I sampled forested plant communities that were dominated by one of these invasive shrubs, as well as a nearby site of similar environment and land-use history with little invader presence. I utilized the methodology of the Carolina Vegetation Survey (Peet et al. 1998, 2012), which employs nested subplots at six spatial grains (Figure 2). I intensively sampled modules 2, 3, 8 and 9, identifying species in nested corners and counting the number of woody stems at breast height in each of those four modules. I collected soil samples from the A horizon of each plot, collecting 250 g of soil at 5-20 cm below the soil surface from each intensively sampled module, and combining the samples for one plot-level representative sample. This sampling resulted in 52 plots: 13 plots each that were dominated by either *L. sinense* or *E. umbellata*, and 13 matched control (uninvaded) plots for each focal invader.

After completion of the field season, collected soils were oven dried at 50^0 C for 48 hours, sieved, weighed, and shipped to Brookside Laboratories Inc. Nutrient analyses employed the Mehlich III method (Mehlich 1984), Total cation exchange capacity (meq/100g), pH, estimated nitrogen release, easily extractable P, exchangeable cations (Ca, Mg, K, Na ppm), and soluble sulfur values were determined for each sample.

To determine additional abiotic correlates of shrub invasion and removal, I returned to 18 of these 52 plots in the summer of 2015. For this study, I collected data in three

replicate plots at six sites: one invaded plot with focal invader removal in the middle of the summer, one invaded plot without removal and one uninvaded control plot. Each of the three plots at each site shared similar species composition, as well as topographic, disturbance, and land-use history characteristics. These three plots provided baseline comparisons of the impact of invaders across the whole study time line, as well as the impact of mechanical removal of the invader midway through the summer.

At each plot, I set out four HOBO environmental data loggers, one in the center of each intensive module at ground level, to record local air temperature (^{0}C) and visible light availability (lumens/m^2) every 15 minutes (for more information on hobo loggers and their uses, see Dunham et al. 2005 and Kennard et al. 2005). Data collection began on 12 May 2015 and continued through 25 August 2015. In addition, I used a Hydrosense Soil Moisture Probe to collect Volumetric Water Content of the soil at 20 cm depth every 3 weeks in 5 locations at each plot (at the center of each intensive module and the intersection of the four intensive modules). This replication within plots provided improved data measurements in case of faulty loggers and demonstrated any impacts of spatial heterogeneity.

In the invaded plots with focal invader removal, I mechanically removed all stems of the focal invader reaching 1.37 m in height, as well as any associated vine stems, via chainsaw from each intensively sampled module, representing 400 m^2 of removal. I cut each stem to below 1 m height and carried all cut stems outside of the plot. This focal invader removal occurred from June 23-25, 2015. An alternative method, removal of invader stems within just one module and comparison to other modules within the same plot, would have allowed for an increased number of invaded-control samples across all my previously sampled plots and more consistent conditions for isolation of the treatment effects. However,

this method would allow for the hypothesized impacts of the removal to affect measurements taken at supposed control loggers (increased light, higher temperature, etc.). This potential confusion of the data, as well as potential confounding impacts caused by mid-season sensor failures or spatial heterogeneity, led to the methodology employed where I compared full plots with differing invasion status, rather than individual modules.

Data Analysis

To determine the differences in abiotic conditions with shrub invasion, I compared data collected in the uncut invaded plots with uninvaded control plots. I calculated the mean temperature and median light availability each day for each treatment plot, as well as the mean soil moisture at each time of sampling in each plot and error distributions for each calculated value, using R version 2.15.1 (R Core Team 2012).

Due to the effects of phenology and seasonality on my time series data, I could not simply compare raw values in cut plots to those same raw values in uncut plots from before and after cutting. Since the cut plots shifted mid-summer from closely resembling the uncut plots to more closely resembling the control plots in physical structure, I took the mean of the two uncut plots to serve as a baseline value for determining the effect of the cutting. I then relativized each site for comparison purposes by dividing the mean temperature of the cut plots by this baseline value. Relativized values >1 indicated that cut sites were warmer than the mean of uncut sites, while relativized values <1 indicated that cut sites were cooler than uncut sites. I relativized the mean temperatures of every sample time in the cut plot, dividing it by the mean of the uncut and control plots for that time. I calculated the mean and standard deviation of these relativized means for each focal species, separating the dates that were before physical removal from those after physical removal. I performed the same relativized

measures with light availability. Due to the much broader range of fluctuation in light readings, however, I calculated the median value of light for all sites, rather than the mean, so as to not have my results skewed by extreme light values. I then calculated the relativized ratio as with temperature, where a ratio of 1 represented an equal amount of light availability in an average day at a given time. I the calculated the standard error of the median light values for each. Finally, I calculated the relativized mean and standard deviation of volumetric water content (VWC) at each cut plot and each sample date using the 5 readings taken in each plot.

In addition to daily temperature and light readings, I calculated the relativized mean value in cut plots at every hour of a typical day. I separated temperature and light values into those prior to cutting and those after cutting, then calculated the mean and error distributions for the relativized means at times prior to cutting and times after cutting. To determine significant differences, I calculated one-way anova values for each calculated mean value of temperature, light availability and soil moisture previously described.

To determine if any individual soil characteristic was reflective of species removal, I calculated the relativized mean ratio of each soil characteristic in cut plots, and I compared the relativized values in cut communities prior to and after cutting, using a one-way anova. These soils were collected at the time of initial plot sampling in summer 2014 and again in November 2015, approximately 5 months after focal invader removal. As with soil moisture and temperature, I relativized the measured soil values to the mean of the uncut invaded and control communities.

Results

Invaded and uninvaded plots did not differ significantly in temperature, light availability or soil moisture across the sampling period (Figure 3). Invaded plots did express visually lower temperatures, lower light availability and higher soil moisture levels throughout much of the sampling period, but these variations were not statistically significant. Generally, plots associated with *Ligustrum sinense*, both invaded and uninvaded, exhibited higher soil moisture readings across the sampling period than plots associated with *Elaeagnus umbellata*.

Ligustrum sinense removal corresponded to significant increases in temperature and light availability, relative to the average of uncut plots (Figure 4). *Elaeagnus umbellata* removal corresponded to a significant increase in light and a non-significant increase in temperature. Mean soil moisture was not significantly different after focal invader removal, though *L. sinense* removal did exhibit a non-significant increase across the sampling period.

While experimental plots were generally cooler and darker prior to experimental removal; removal yielded a marked increase in both hourly temperature and light (Figure 5). *L. sinense* removal demonstrated a significant increase in hourly temperature ratio across the day (10 AM-5 PM), compared to significant increases only during peak temperature readings (2-4 PM) for plots with *E. umbellata* removal. Excepting the first and last hours of sun exposure in a day, removal of both focal invaders significantly increased light availability in removal plots across the day.

Ligustrum sinense removal corresponded with significant decreases in potassium and significant increases in sodium (Figure 6). *E. umbellata* removal corresponded with significant decreases in potassium and sodium and marginally significant decreases in

magnesium. No other soil measurements demonstrated significant change with focal invader removal.

Discussion

The lack of significant differences with invasion in temperature, light, or soil moisture likely reflects the similarity of invaded and uninvaded plots among landscape-scale metrics, such as slope, aspect, and topographic position. These broad environmental conditions often correlate with significant factors for plant survival and growth, such as temperature, light and moisture (Siccama et al. 1970, Bennie et al. 2006). Because paired invaded and control sites were typically more similar to one another in environmental conditions relative than to other plots with the same invasion distinction, these temperature and light variations, though qualitatively noticeable between plots, were not statistically significant. The increased soil moisture levels in both invaded and uninvaded *Ligustrum sinense* plots relative to *Elaeagnus umbellata* plots likely reflects their riparian nature where soils are more often saturated due to increased water inputs. The upland communities typical of *E. umbellata* invasion in the southeast, by contrast, lose rainwater through surface and groundwater runoff, yielding lower mean soil moisture across the growing season.

The significant, though limited, increases in both mean daily temperature and light with focal invader removal likely reflect the role these dense shrub layers play in community structure. Although shrub presence and absence are visibly noticeable in forested communities, these species often did not receive a significant amount of direct sunlight in the sampled plots. The increase in daily light availability with focal invader removal, while significant, reflects previous findings of additional resources for native competitors (D'Antonio et al. 1998). However, the invasion of exotic shrub species into predominantly

closed-canopy forests suggests that these invaders are competing with other understory species in already-low light environments (Chazdon and Pearcy 1991, Messier et al. 1998) and their subsequent removal is not as drastic as would be the removal of overstory trees.

Similar patterns of resource use likely explain the non-significant changes in soil moisture due to focal invader removal. The greater effect of *L. sinense* on temperature and light availability may be due to its greater densities in invaded communities than *E. umbellata* (Chapter 3), thus reflecting an increased opening of the sub-canopy with its removal. It should be noted, however, that the coarse soil moisture measurements used in this study, representing only six samples across 18 weeks, may have missed more nuanced changes in moisture readings with invasion and subsequent removal. Although the broad-scale patterns did not change, more immediate change to the surface level moisture availability may have occurred beyond the scope of these measurements (D'Antonio et al. 1998).

No soil characteristics changed in a manner that has been ascribed to the life history or physiology of these specific shrubs (see Goldstein et al. 2009), and changes in soil nutrients did not reach levels matching toxicity or deprivation (Brady and Weil 2007). Thus, the impacts of these changes on the biotic communities are likely small, if quantifiable at all. It is likely that the impact of shrub removal was diminished in temperate broadleaf forests relative to other systems, due to the significantly greater biomass occupied by canopy and mid-story trees. Similarly, the changes documented here are reflective of relatively coarse soil measurements, taken at only two sample dates across an 18-month study period. These measurements do not encapsulate the long-term flux of nutrients or the immediacy of nutrient availability change associated with invasive species management, which might provide a

more complete depiction of such changes in a broad ecosystem context (see Ehrenfeld 2003 for a review).

The abiotic changes with removal determined in this study likely will cause future corresponding biotic responses, though the magnitude and direction of such changes are difficult to predict. Removal of dominant exotic species may foretell long-term abiotic responses, such as changes to soil moisture regimes or soil pH (Hartman and McCarthy 2004). The disturbance generated by physical removal, however, may instead facilitate further success of invasive exotic species via changes to light and resource availability (Parendes and Jones 2000; Davis and Pelsor 2001). The dominant exotic species could re-establish quickly in these systems, particularly due to its continued proximity to propagules (D'Antonio et al. 2001). As is the case with abiotic responses to both shrub invasion and removal, biotic responses will likely be nuanced and context-dependent, with time-lags in quantifiable change compounded by additional community interactions. Nonetheless, these data indicate that forested communities are quantifiably changing due to shrub invasions.

Conclusion

Shrub invasions do not cause significant impacts on community environmental characteristics, though there are non-significant changes in temperature and light, likely due to the emergence of a dense shrub layer. Removal of these shrubs yielded significant changes in temperature and light, but few changes in soil moisture or nutrients. This is likely due to the minor role shrub species play in resource uptake in closed-canopy forests, relative to larger overstory trees.

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Tables and Figures

Figure 1. Geographic distribution of 52 sampled communities in a paired-plot empirical design, WNW of Charlotte, NC. 13 plots each were invaded by either *Ligustrum sinense* or *Elaeagnus umbellata*, each with a paired plot nearby.

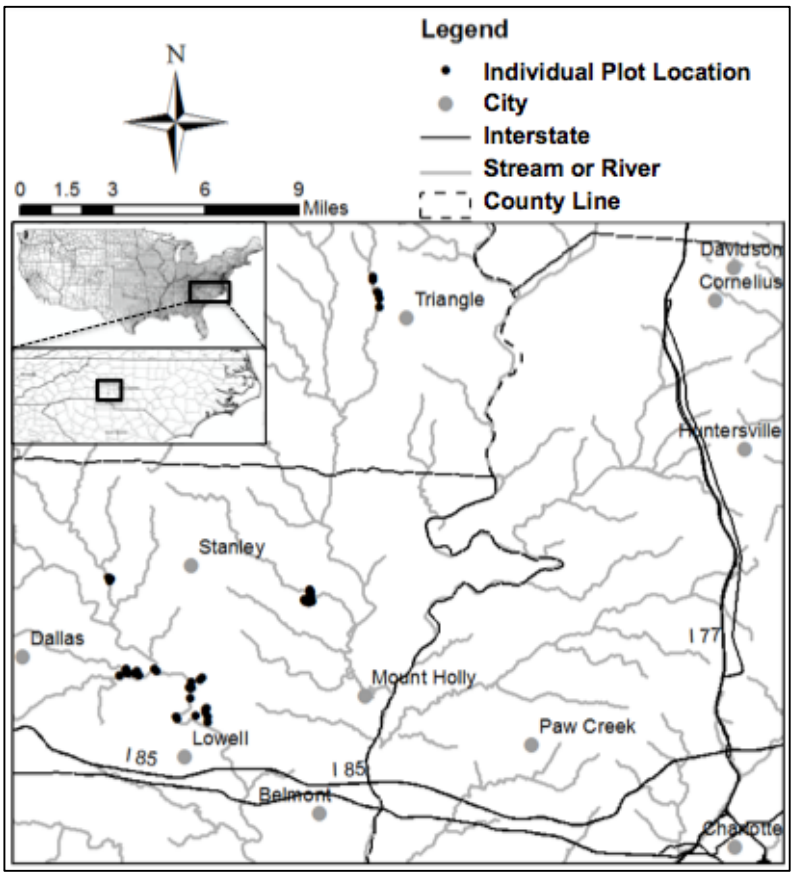

Figure 2. Plot design for CVS methodology, with 10 modules, each 10x10 m. This study examined abiotic relations in the four intensively sampled modules (represented here with their intensively sampled corners). Hobo light and temperature trackers were placed in the center of each of the four modules, and soil moisture readings were taken every three weeks by each tracker, as well as at the intersection of the four modules. (Reproduced from Peet et al. 2012)

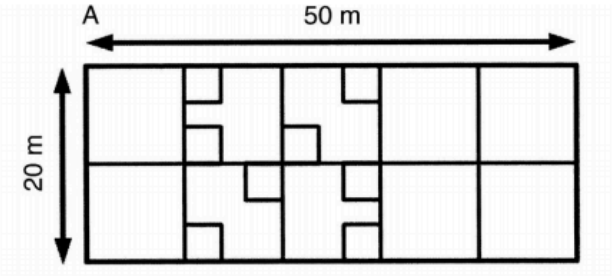

Figure 3. Comparison of temperature, light and soil moisture ratio between invaded and uninvaded plots for each focal invader. Each line in each figure corresponds to one paired-plot site for that focal invader. There is no statistically significant difference in any metric for either focal invader with invasion across the sampling period, though there are non-significant differences with invasion that are consistent among the two species, namely decreased temperatures and light availability and increased soil moisture.

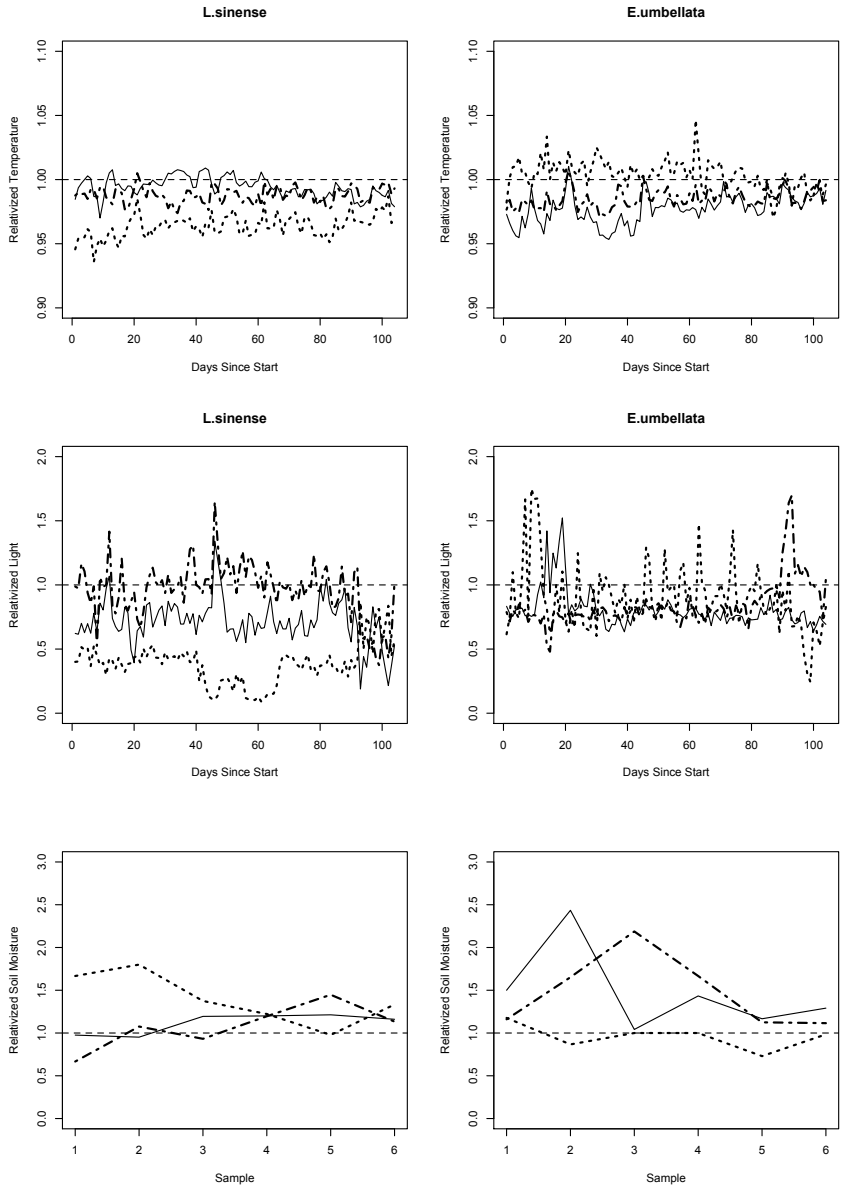

Figure 4. Change in daily relativized temperature, light and soil moisture ratios across the sampling season due to experimental removal of the focal invader, comparing the measured values in experimental plots to the mean of the invaded and control plots with no experimental removal. Vertical dashed lines correspond to the time of experimental removal, and horizontal dashed lines correspond to variance in the mean ratio for a given date. *Ligustrum sinense* removal corresponded to significant increases in temperature and light availability, as well as a non-significant increase in soil moisture, relative to uncut plots. *Elaeagnus umbellata* removal corresponded to a significant increase in light and a non-significant increase in temperature, but no change in soil moisture.

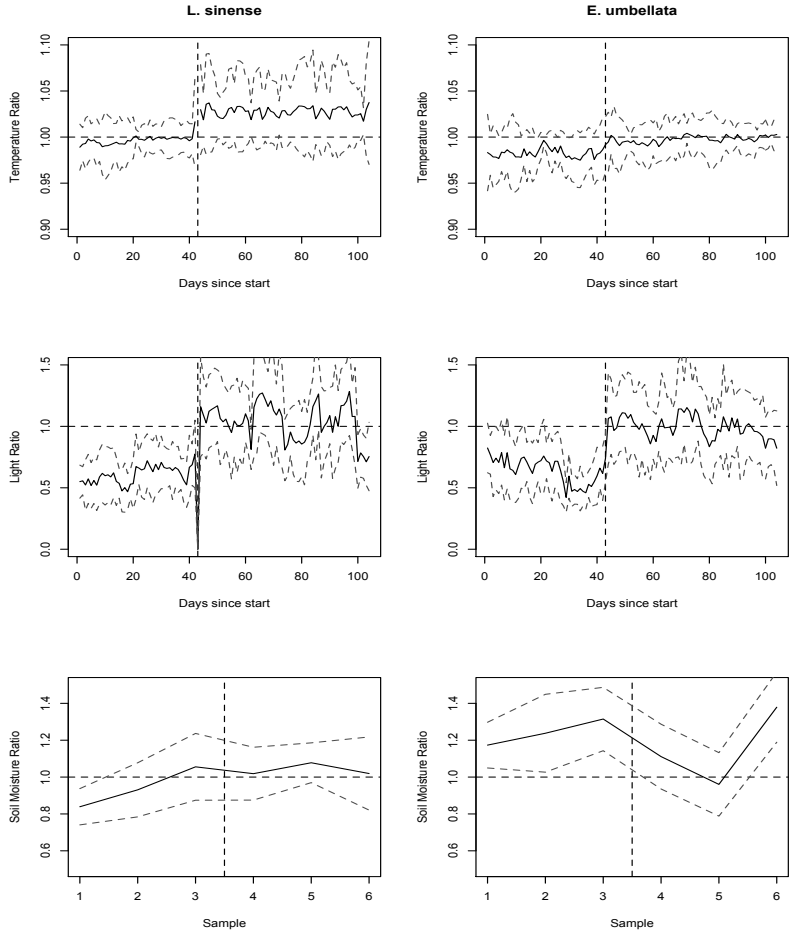

Figure 5. Change in hourly relativized temperature and light ratios due to experimental removal of the focal invader, comparing the measured values in experimental plots to the mean of the invaded and control plots with no experimental removal. While experimental plots were generally cooler and darker prior to experimental removal, removal yielded a marked increase in both temperature and light. *Ligustrum sinense* removal demonstrated a significant increase in hourly temperature ratio throughout hours of peak irradiance (10 AM-5 PM), compared to significant increases between (2 and 4 PM) for plots with *E. umbellata* removal. Excepting the first and last hours of sun exposure in a day, removal of both focal invaders significantly increased light availability in removal plots across the day.

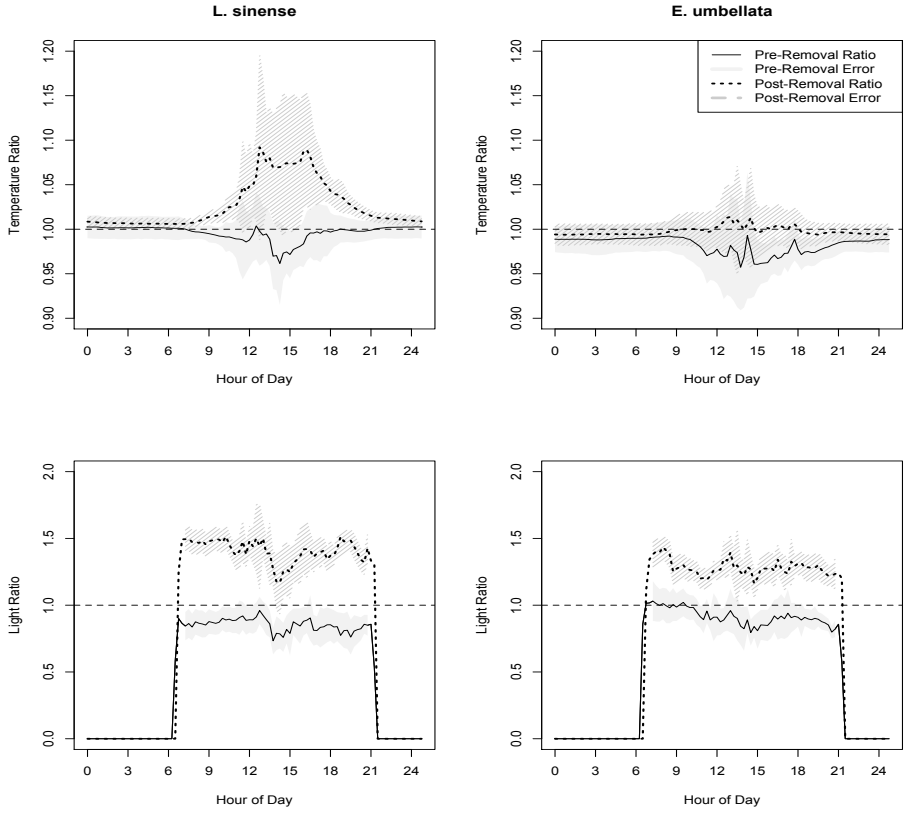

Figure 6. Changes in prominent soil nutrient levels due to experimental removal of the focal invader, comparing the measured values in experimental plots to the mean of the invaded and control plots with no experimental removal. Samples taken in 2014 correspond to 1 year prior to invader removal, and samples taken in 2015 correspond to 5 months after invader removal. (A) *Ligustrum sinense* removal corresponded with significant decreases in potassium and significant increases in sodium. (B) *Elaeagnus umbellata* removal corresponded with significant decreases in potassium and sodium and marginally significant decreases in magnesium. No other soil measurements demonstrated significant change with focal invader removal.